MASTERARBEIT

Titel der Masterarbeit

„Impact of flood control on communities of meadow butterflies in the Nationalpark Donau-Auen“

verfasst von

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„Jedes Naturgesetz, das sich dem Beobachter offenbart, lässt auf ein höheres, noch unerkanntes schließen.“

Alexander von Humboldt

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Introduction

The "Nationalpark Donau-Auen” ranges as a green belt between the congested areas of the capital cities Vienna and Bratislava along the Danube River. It represents the biggest remaining functional riparian environment of Central Europe, on a total area of 9.300 ha (NATIONALPARK DONAU-AUEN GMBH 2014). The National Park was accredited by the IUCN in 1997, even though it does not fulfil the criterion of zonation according to the strength of conservation and management regulations. For example a buffer zone could not be allocated because the Nationalpark Donau-Auen is directly adjacent to residential areas. Instead of having a core area, the reserve is divided into the “nature zone” with and without management, respectively (NATIONALPARK DONAU-AUEN GMBH 2014a) .

All extant meadows in the Nationalpark Donau-Auen are secondary relicts of former anthropogenic land-use like grazing of farm animals or harvest of hay. Nowadays they are irreplaceable elements of a cultural landscape, increasing the ß-diversity enormously. These meadows provide several additional habitats that differ above other ecological aspects in the frequency and duration of inundations and the mowing regime.

Since the Danube near Vienna is an alpine river, the regular flooding events result from the snowmelt in the Alps normally happening between June and July (TOCKNER *et al.* 1998). The construction of a continuous levee (“Marchfeld-Schutzdamm”) in the late 19th century interrupted flooding dynamics in the northern part. In the southern part, fluctuations of the water level of the Danube may reach up to 7 meters in extent and water flow through ranges between 1,500 - 1,900 m^3/s at average water level. In August 2002 an extreme flooding event was reported, with a water supply of 11,000 m^3/s and a water level of 7.80 m near Orth an der Donau, which was still exceeded by the flood in 2013 with 11,000 m^3/s and 7.98 m (LEBENSMINISTERIUM VII/3).

Mowing is done by third parties through contractual conservation management agreements twice a year in June and August with the objectives of “preserving the different types of meadows, rare plant species, and structural elements for animals and to maintain the natural scenery”. Meadows with low productivity are mown once a year. It is stipulated that the harvest (freshly cut or as hay) has to be removed from all mown meadows. In some years, mowing may be prevented or interrupted by flooding events, mostly in early summer at the first mowing date (NATIONALPARK DONAU-AUEN GMBH 2009).

As is typical in Central Europe, butterfly communities are more species rich on meadows than in closed-canopy forest due to the high thermal demands of these organisms. On the one hand, they are highly mobile during their adult stages, making fast reactions to abiotic factors and recolonization after local population extinctions possible. On the other hand, caterpillars are sedentary and trophically linked to one (monophagous spp.) or a few (oligophagous spp.) host plant genera (CIZEK *et al.* 2012). Hence, flooding as well as mowing constitutes major mortality factors for caterpillars.

In Central Europe, the impacts of flooding regimes on terrestrial arthropods in general and on butterfly communities in particular have not been in the focus of many research projects yet (TRUXA & FIEDLER 2012). Insects of flooded areas have to deal with low oxygen concentration during inundations, the destruction of local habitats and the risk of passive drift away from their microhabitats (ROTHENBUECHER & SCHAEFER 2005). Some species, like the butterflies *Lycaena dispar batavus* and *Coenonympha tuilla* are adapted to submergence by climbing up their host plants as larvae (JOY & PULLIN 1997, NICHOLLS & PULLIN 2003). In both species, tolerance to submergence has been shown to be variable. Studies on *L.dispar batavus* revealed that not only the duration of an inundation influences mortality, but also the exact stage of development which experiences flooding. Early diapause larvae of *L. dispar* batavus suffered 50% mortality after 90.8 days, whereas the same happened to late diapause larvae after only 19.4 days under water. If only partially flooded, immediate mortality was not significantly higher than in controls (NICHOLLS & PULLIN 2003). In *C. tullia* a direct mortality of 50% after 7 days of submergence was followed by sublethal effects, whose causes could not be identified (JOY & PULLIN 1997). An increasing indirect mortality was also found in *L.dispar batavus*, whose larvae were not capable to finish development successfully after being exposed to a flooding event (Webb & PULLIN 1998). Hibernating larvae of *Neptis rivularis*, which also inhabits wetlands did not even survive 21 days of inundation (KONVICKA *et al.* 2002). The eggs of *Lycaena epixanthe* show adaptions to submergence. Spines on their eggs surface are able to trap air, which might than be respired by the egg (WRIGHT 1983). SEVERNS *et al.* (2006) supposed the same egg surface for another wetland species, *Lycaena xanthoides*. Concluding the findings of several studies on the listed wetland butterfly species *C. tuilla, L. dispar batavus, L. epixanthe L.xanthoides* and *N. rivulars,* SEVERNS *et al.* (2006) stated that even though these species are supposed to be adapted to inundations, all of them still show a higher survival in habitats without inundation. According to them this proves that all these species are either not yet completely adapted or just as adapted as physiologically possible.

In floodplains at the rivers Danube, Morava and Leitha regional aspects like different habitat conditions were shown to a have a bigger influence on moth diversity than the local flood regime (TRUXA & FIEDLER 2012). Total moth diversity in forest habitats influenced by regular floods was even higher (TRUXA & FIEDLER 2012), which is contrary to the Rhine floodplains where more moth species where found in forests not prone to frequent inundations (KÖPPEL 1997). However regarding only moths with early stages in the ground-layer, inundations had a negative influence on species diversity compared with non-flooded regions (TRUXA & FIEDLER 2012). Also ants, which are living directly on and in the ground, revealed a lower species richness in flooded regions (BALLINGER *et al.* 2007). Contrary to expectation, at the Danube a characteristic moth community with species that show more tolerance towards inundations was not found (TRUXA & FIEDLER 2012). Such was also not the case in spider communities (VAN HELSDINGEN 1997). BALLINGER *et al*. (2007) stated that most terrestrial arthropods which inhabit floodplains were ubiquitous opportunists, which were able of fast recolonization after catastrophic events.

The role of mowing as a method to avoid the encroachment of bushes in anthropogenic, open landscapes has widely been discussed in conservation biology (GERSTMEIER & LANG 1996, MORRIS 2000, GRIME 2006). Whereas mowing may be seen as an essential step to maintain different types of meadows with a low nutrient content, fewer shrubs and more rare plant species, it is also a catastrophic event for ground-layer insects. Even though mowing is expected to influence invertebrate diversity negatively, still no consensus has been reached as to its effects on insects in general and butterflies in particular (HUMBERT *et al.* 2009, DOVER *et al.* 2010). On the one hand adult butterflies may easily escape by flight, while eggs, larvae and pupae rely on unmown patches, including their host plants, for survival (HORN 2012). Local populations not only have to deal with direct mortality of the immobile stages, caused by the mowing event (HUMBERT *et al.* 2009). Mowing also changes habitat structures thereby influencing the availability of oviposition sites (either positively or negatively), and leads to a temporary shortage of nectar sources (DOVER *et al.* 2010). To make things even worse, mowing is often done in the mornings, when temperatures are not high enough to allow adult butterflies to escape. That is why DOVER *et al.* (2010) actually concluded direct mortality to act on the mobile, adult stages as well. KONVICKA *et al.* (2008) stated that mowing has to be adapted to the “gradual and patchy manner” like otherwise extensive grazing or sythe-mowing may obtain. Additionally a mosaic of cut and uncut swards may be a solution (HUMBERT *et al.* 2009). The cutting time and interval may also modify the effects of mowing on different species. JOHST *et al.* (2006) found that *Maculinea nausithous* tolerates a variable span concerning the mowing week (in the year), if each meadow is only cut every second or third year. How severely the influence of hay harvesting may affect butterflies was shown by KONVICKA *et al* (2008). In the Carpathians and the Czech Republic they detected that blindfold grassland management through uniform machine mowing for more than ten years drove a formerly stable population of *Colias myrmidone* to extinction. In conclusion one can say that the effects of mowing on local butterfly diversity and population persistence (CIZEK *et al.* 2012) not only depend on the mowing regime, but also on the landscape and the traits of the respective species (JOHST *et al.* 2006).

Even if not researched extensively, disturbances like the inundation or mowing events cause ecological alterations not only in species diversity but also in functional diversity (NAEEM 2002), making it an essential component for conservation planning (DÍAZ *et al.* 2007). By using a functional diversity index FD (PETCHEY & GASTON 2006), FLYNN *et al.* (2009) reported an even steeper decline in functional diversity than in species diversity on bird and mammal species caused by land-use intensification. Also functional diversity on two tropical amphibian communities declined strikingly after selective logging, even though species-diversity did not differ significantly (ERNST *et al.* 2006). Functional diversity has been shown to describe species assemblages rules in several studies (MASON *et al.* 2005, CORNWELL *et al.* 2006, MCGILL *et al.* 2006, MASON *et al.* 2007). Using simulated communities MASON *et al.* (2010) found that, besides others of the numerous functional indices categorized in recent years (i.e. PETCHEY *et al.* 2004, RICOTTA 2005, PETCHEY & GASTON 2006, SCHLEUTER *et al.* 2010), the three orthogonal indices Functional Richness, Functional Evenness and Functional

Divergence are sensitive on local community assembly rules (Mouchet *et al.* 2010). There are three theories used to describe local species assemblies, which may co-occur as described in Mason *et al.* (2007) and Helmus *et al*. (2007). The first theory, called niche filtering, assumes that environmental constraints act as filters, forcing species with similar but optimal functional traits to coexist (Zobel 1997, Cornwell *et al.* 2006). Environmental filtering was proven to be stronger in a regional scale (Díaz *et al.* 1999, Cornwell *et al.* 2006). In contrast to that the limiting similarity theory, a modification of the competitive exclusion principle, stats that only up to a maximum, similar species may coexist (Abrams 1983). Local assemblies driven by the limiting similarity are inhabited by functionally complementary species to avoid competition (MacArthur & Levins 1967, Mouillot *et al.* 2007). Placed in between these theories, the neutral theory (Hubbell 2001) stats that overlapping niches are possible, as species and individuals are equivalent. Community assembly is rather driven by the events of ecological drift, migration and speciation (Beeravolu *et al.* 2009).

Functional diversity may be optimally described by three indices Functional Richness, Functional Evenness and Functional Divergence, which were proven to be independent of each other several times (Villéger *et al.* 2008, Mouchet *et al.* 2010, Pakeman 2011). Functional Richness represents the amount of trait space occupied by species (abundance is not included) of the community. Low values of Functional Richness demonstrate that some niches in the functional space are not occupied. Unused niches multiply the chances of invasion (Dukes 2001, Mason *et al.* 2005, Mouchet *et al.* 2010). Functional Evenness describes the regularity of the species and their abundances in the functional trait space. Therefore, low values suggest that some areas of the functional space are crowded while others are not filled at all (Mouchet *et al.* 2010). Pakeman (2011) showed with plant communities that Functional Evenness increases in disturbed areas. Mason *et al.* (2008) described Functional Divergence as the “abundance-weighted functional differences between the species within a community”. High values of Functional Divergence imply that the most abundant species have traits on the outer margin of functional space (Villéger *et al.* 2008), indicating a high degree of niche differentiation, an efficient resource usage and correspondingly low resource competition (Mason *et al.* 2005).

The first aim of this study was to provide an exhaustive butterfly species list to the Nationalpark Donau-Auen, including a variety of data sets (1). Secondly, this study aimed on establishing the influence of inundation on butterfly communities. Species numbers and total abundances are expected to be lower on meadows which are flooded regularly. Also species composition might differ because of flooding regime. Species thriving on flood-prone meadows might be ubiquitous opportunists as described for arthropods (Ballinger *et al.* 2007) or specialists for humid habitats. There might be differences in feeding guilds, due to habitat preferences and adult life-history traits (2). Similarly, mowing might influence butterfly species richness, abundance and species composition. Those meadows that are not mown might reveal a lower species number and abundance, as certain larval host plants might be missing and nectar resources become more limited during succession (3). Finally, I will analyse whether Functional Diversity of butterfly assemblages differs according to flooding or mowing regimes with emphasis on the food and habitat niche as well as the resilience and fragility of the species (4).

Material and Methods

Study sites and sampling

In the Nationalpark Donau-Auen 20 meadows in the northern part and 18 meadows (Fig. 1) situated south of the levee were periodically sampled five times each, from the end of April until the middle of September 2013.

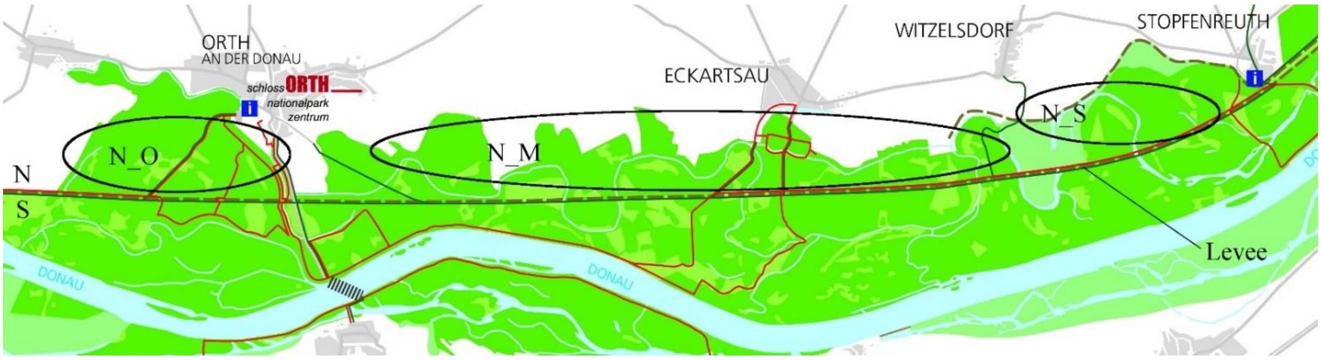

Fig. 1. Schematic representation of the study area and the different flooding categories on the northern and southern part of the levee. N = northern meadows, further categorised as N_O = seven meadows, situated near Orth an der Donau, which experienced uprising groundwater, N_M = nine meadows, which did not experience any influence of the flood, N_S = four meadows near Stopfenreuth that were actively. S= 18 southern meadows, that are annually flooded. The map was kindly provided by the Nationalpark Donau-Auen and altered.

There was a break of at least three weeks between each sampling round. Meadow area ranged between 0.3 and 5 ha, but most had an area of about 1.3 ha. Sampling was only done if weather was dry, air temperature was at least 17°C if overcast (or 13–17°C during sunny weather) and not windy (≤ 4 Beaufort). A time-standardised survey method was used (Tab. 1). Butterflies were recorded in a 5 m radius to the front, walking in "zigzaggs" as described in (Tropek & Konvicka 2010). If necessary butterflies were netted, identified after the standardized sampling time using Slamka (2004) and Stettmer *et al*. (2011) and released again. The sibling species *Leptidea juvernica* and *Leptidea sinapis,* as well as *Colias alfacariensis* and *Colias hyale* were not further identified, due to unreliable identification in the field, at all used datasets.

Table 1. Standardised transect sampling time relative to meadow area.

area in ha	time in min
0.5	20
1	20 + 15
1.5	20 + 15 + 10
2	20 + 15 + 10 + 5
2.5	20 + 15 + 10 + 5 + 2.5
3-5	20 + 15 + 10 + 5 + 2.5 + 1.25

Predictors

The park area was separated into the northern, not normally flooded habitats (N) and the southern, annually flooded habitats (S). Exceptionally, however, the intense flood of 2013 influenced even some of the northern meadows. Therefore, the northern meadows were additionally separated into three categories. N_O refers to seven meadows, situated near Orth an der Donau, which experienced standing but clear water for over two weeks because of uprising groundwater N_M refers to nine meadows, which did not experience any influence of the flood at all. In contrast, four meadows near Stopfenreuth (N_S) were actively flooded because this region serves as a flood retention basin (Fig. 1). The time and completeness of mowing of the meadows was recorded during the whole survey. Sites were classified as mown (with grass removed), mulched, or not mown. On each meadow and during each sampling period, the amount of available nectar sources was scored on a scale from 1 (poor) to 3 (rich). For further analyses the average of the nectar source scorings of all five sampling periods was used. The area of the sites was extracted from a geographic information system using ArcMap 10 (ESRI, 1999-2010). For all meadows (except one) a plant species list and a phytosociological classification of the meadows was provided by the Nationalpark Donau-Auen. In order to get a coarse index for the nutrient level of the meadows, the average of the Ellenberg indicator values for nitrogen of the eponymous species of the plant communities present on each meadow was used.

Analysed datasets

Additionally to the 2013 butterfly surveys, datasets from the years 2012 (RABL 2012) and 2005 (FIEDLER, pers. comm.) were analysed. In the 2012 survey, 14 meadows to the north of the levee corresponding to northern meadows from 2013 and 13 south of the levee, corresponding to southern meadows from 2013, had been investigated. In contrast to the 2013 survey, meadows in 2012 and 2005 were only sampled twice. In 2012 sampling took place in June, before the inundation (which was short and rather weak) and in July after the inundation. In the 2005 survey, 12 northern and 16 southern meadows were analysed, but only five in the northern part and six in the southern part corresponded to meadows studied in 2013. Five of the northern meadows were sampled in May and June, seven only in May. In the southern part seven of the meadows were sampled twice (in May and June) and nine once in June. Only for the 2012 survey, environmental descriptors (flood, mowing, nectar, nutrient level, area) comparable to the 2013 survey were available.

Data analysis

Statistical analyses were done using the free software R (R CORE TEAM 2013). All datasets were graphically tested for normal distribution using quantile-quantile plots as implemented in the package CAR (FOX & WEISBERG 2011). To meet normal distributions more closely, the data was square-root or arcsin square-root transformed if necessary.

Species accumulation curves were calculated using rarefaction, as implemented in the package VEGAN (OKSANEN *et al.* 2013). The program SPADE (CHAO & SHEN 2009) was used to estimate the sample coverage error and the number of missing species, applying the Incidence-based Coverage (ICE) which uses the group of rare species for estimating the expected total species richness of a site (COLWELL & CODDINGTON 1994, COLWELL 2006).

General linear models (GLM) were applied, using the package STATS (R CORE TEAM 2013). The influence of the aforementioned predictors was tested on a range of response variables that characterize various aspects of butterfly community composition. These included: 1. Number of recorded butterfly species and individuals (both square-root transformed) 2. Percentage of grass, herb, wood, Fabaceae or Brassicaceae feeding species to the overall butterfly abundance of each meadow, 3. Percentage of individuals representing species from three habitat preference classes (living predominantly in meadows, margins and meadows, or woody habitats), 4. Percentage of individuals belonging to species with very low (40-89 eggs), or very high (304-1024 eggs) fecundity, 5. Percentage of individuals representing migratory, very dispersive species or species showing strong side fidelity, 6. Percentage of individuals representing species with a very long lifespan (> 36 day) and 7. Percentage of individuals representing mono- and polyvoltine species. Species trait data were extracted from BINK (1992) and SETTELE *et al.* (2005). All proportions were arcsin square-root transformed. Also the influence of the selected predictors on the butterfly community temperature index and analogous measures of the butterflies' climatic niches relative to precipitation and soil water content (SCHWEIGER *et al.* 2014) were analysed using GLMs. For all GLMs an automatic model selection (backward and forward), using AICc as criterion, was computed using the package STATS (R CORE TEAM 2013). Predictors which were removed from the best model are hereafter marked with n.i. (not included). Only models showing any significant relationships were subjected to interpretation. Statistical significance for all tests was set to $p \leq 0.05$. For continuous predictors the standardized regression coefficient (β) was used to clarify, if the relationship between the variables was positive or negative, using the package QUANTPSYC (FLETCHER 2010).

Non-metric multidimensional scaling (NMDS) was done to display the species composition, (Bray-Curtis similarity matrix), as implemented in VEGAN (OKSANEN *et al.* 2013). Vectors indicating relationships with environmental predictors were a posterior fitted into the ordinations, calculated as Spearman’s rank correlation coefficients between ordination axis scores of the communities and the respective predictor values. Besides the predictors already described above, the two ordination axis scores of the plant species community (presence/absence) were used. Only predictors showing significant influence ($p < 0.1$) on the species composition were used, as only the predictor flood showed a highly significant influence of ($p < 0.005$). Multivariate Analysis of Variance (MANOVA) (VEGAN, OKSANEN *et al.* 2013) based on a permutation was done to test the influence of the predictors on species composition. For the NMDS ordination of both years, species which could not be found in the 2012 survey, because of early flying times were removed from the dataset (*Anthocharis cardamines, Zerynthia polyxena*). Analysis of similarities (ANOSIM) was performed to test, whether there were significant difference between the species composition of the different flooding regimes and the years (vegan, OKSANEN *et al.* 2013).

Graphics were done using the package GRAPHICS (R CORE TEAM 2013) and GGPLOT2 (WICKHAM 2009).

Functional Diversity

10 functional traits were used to calculate the Functional Diversity Indices, consisting of categorical parameters on the food niche of caterpillars, the phagism (BINK 1992) the type of food plants, the habitat of the caterpillars taken from SETTELE *et al.* (2005), detailed information on the climatic niche of the species, the average annual temperature, the average precipitation and the average soil moisture (SCHWEIGER *et al.* 2014), the lifespan, voltinism, fecundity (SETTELE *et al.* 2005) and the length of the forewing (SLAMKA 2004) (Tab. 19).

Functional Diversity indices were calculated using the package FD implemented in R (LALIBERTÉ & LEGENDRE 2010, LALIBERTÉ & SHIPLEY 2011). All traits were standardized to mean 0 and unit variance, like recommended by VILLÉGER *et al*. (2008). A “cailliez” - correction method was performed (CAILLIEZ 1983). A Gower distance matrix was calculated because qualitative and quantitative date were used together (VILLÉGER *et al.* 2008, LALIBERTÉ & LEGENDRE 2010). First a principal coordinates analysis (PCoA) was applied on the species-species distance matrix. Than the PCoA axes were used as traits to calculate the indices. To get a value between 0 and 1, Functional Richness was standardized by the ‘global’ Functional Richness including all species as described by LALIBERTÉ & LEGENDRE (2010). GLMs and a stepwise model selection were performed, testing if the predictors described above had an influence on the three Functional Diversity indices.

Results

In total 4,320 sightings of 63 different species were recorded on the 38 meadows in 2013 (Table 16). The family Nymphalidae represented the highest proportion of species with 44 %, followed by the Lycaenidae (25 %), Pieridae (16%), Hesperiidae (11 %) and Papilionidae (4%).

In the 2012 survey 4,224 sightings of 53 different species were recorded on 27 meadows (Table 17). Also in this year the family Nymphalidae represented the highest proportion of species with 44 %, followed by the Lycaenidae (26 %), Pieridae (15%), Hesperiidae (13 %) and Papilionidae (2%).

In 2005 1,772 sightings of 40 different species were reported on 28 meadows (Table 18). Again the family Nymphalidae represented the highest proportion of species with 41 %, followed by the Lycaenidae (25 %), Pieridae (13%), Hesperiidae (18 %) and Papilionidae (3%).

Species which were uniquely seen in the 2013 survey on one of the northern meadows are *Heteropterus morpheus*, *Polyommatus dorylas, Apatura iris* and *Neptis rivularis* as well as *Polyommatus semiargus* on one of the southern meadows. Additionally *Iphiclides podalirius*, *Anthocharis cardamines*, *Cupido alcetas, Cupido decoloratus* and *Argynnis aglaja* were not found in the 2012 and 2005 surveys, but several times in the 2013 survey on northern and southern meadows (Tables 14, 16).

Only seen in the 2012 survey were *Neozephyrus quercus* and *Thecla betulae,* both seen once on a northern and once on a southern meadow, respectively (Table 14, 17). Only in the 2005 survey, *Carterocephalus palaemon* was found once on a northern and once on a southern meadow. *Aricia agestis* was a unique on a northern meadow (Table 14, 18). *Satyrium pruni* was seen once on the southern side in the 2012 survey and once on the northern side of the 2005 survey (Tables 14, 16, 17).

Additionally 13 species are included in the species list (Table 14), because they have been recorded in the Viennese part of the National Park (HÖTTINGER *et al.* 2013) and are therefore expected to possibly occur in Lower Austria as well.

Species accumulation curves

Species accumulation curves were separately calculated for the regularly flooded meadows north of the levee and those to the south of the levee using datasets collected in the years 2013, 2012 and 2005 (Fig. 2a). In all three years butterfly species richness was higher on the northern meadows. Only the species accumulation curve of the southern meadows in the year 2013 (dark blue line, Fig. 2a) reached saturation. For these meadows additional sampling sites would not add a higher number of species. ICE estimations revealed estimated sample coverage for infrequent species of 0.92 and the number of 9.8 species to be missing on the northern meadows of the 2013 survey (dark red line, Fig. 2a). Additionally species accumulation curves of the northern and respectively the southern meadows using the dataset of all three years (2013, 2012 and 2005) were calculated (Fig. 2b). Again, the butterfly species richness was higher on the northern meadows, but both curves did not reach saturation. ICE estimations revealed a coverage error for rare species of 0.91 and the number of 11.2 species to be missing on the northern meadows of all years and a coverage error of 0.95 and the number of 6.1 species to be missing on the southern meadows of all years. Fig. 3 shows species accumulation curves, using only the datasets recorded in the sampling periods after summer inundation. In contrast to Fig. 2a and Fig. 2b, the surveys from 2012 (a year with a short and moderate flood event) in the northern (pink line) and southern part (turquoise line) revealed higher species richness than in 2013. This indicates a distinct short term decline in species richness after the exceedingly intense flooding event in 2013.

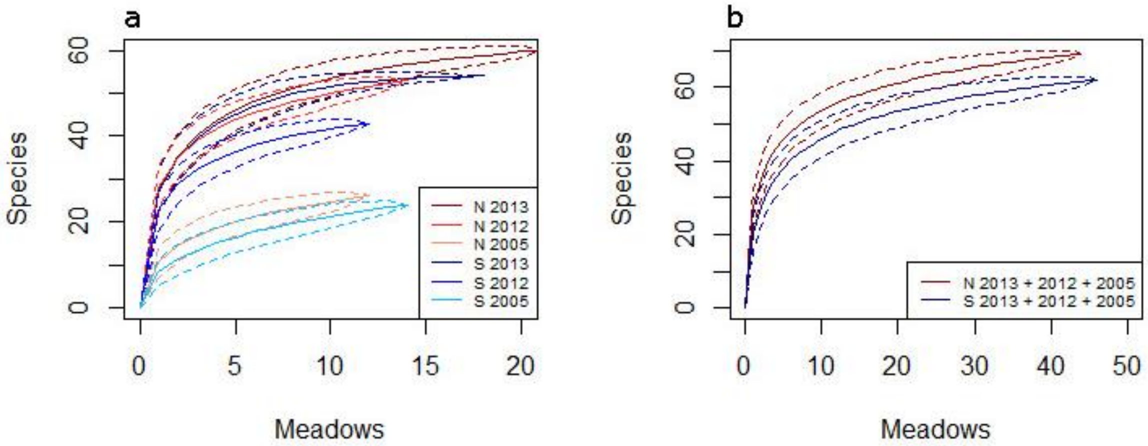

Fig. 2. Randomized species-accumulation curves (method: rarefaction) for (a) the northern (N) and southern (S) meadows of the years 2013, 2012 and 2005 (solid lines), dashed lines: 95% confidence-intervals, (b) the northern and respectively southern meadows, using the datasets of all three years (solid lines), dashed lines: 95% confidence-intervals.

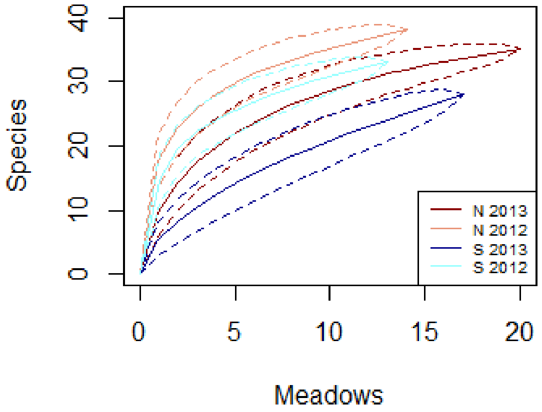

Fig. 3. Randomized species-accumulation curves (method: rarefaction) for the northern (N) and southern (S) meadows of the years 2013 and 2012, using only the datasets recorded in the sampling periods after summer inundation (solid lines), dashed lines: 95% confidence-intervals.

Local butterfly species richness and abundance

The number of recorded butterfly species per meadow was highly significantly related to the number of individuals sighted on the sites in both years (Table 2a, c). Surprisingly, none of the other predictors tested had any relation to observed species numbers in both years. Figs. 4a and 5a show that butterfly abundance was significantly influenced by the flood regime in 2013 (Table 2b) and in 2012 (Table 2d). Total butterfly abundance was also marginally positively related to meadow area in both years (2013: β = 0.242; 2012 β = 0.246). Distinctly more individuals were found on meadows with higher availability of nectar (2013: β = 0.451; 2012: β = 0.615). Only in 2013 butterfly abundance was significantly higher on nutrient poor meadows (Table 2b, Fig. 4b).

Table 2. Results of general linear models, testing the effects of several predictors on (a) butterfly species richness in the year 2013, (b) abundance in the year 2013, (c) butterfly species richness in the year 2012, (d) abundance in the year 2012. Significance codes: '*' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$. Significant effects ($p < 0.05$) in bold case.**

a

number of species, 2013	Df	F	p		
flood	3	2.022	0.135		
mowing	2	0.300	0.743		
nectar	1	1.499	0.231		
area	1	0.021	0.885		
nutrient level	2	0.165	0.849		r^2adj=0.7768
abundance	**1**	**30.593**	**< 0.001**	***	

b

abundance,2013	Df	F	p		
flood	**3**	**4.290**	**0.013**	*	
mowing	2	0.155	0.857		
nectar	**1**	**6.356**	**0.018**	*	
area	**1**	**9.730**	**0.004**	**	r^2adj= 0.652
nutrient level	**2**	**6.093**	**0.006**	**	

c

number of species, 2012	Df	F	p		
flood	1	0.006	0.938		
mowing	2	0.644	0.537		
nectar	1	4.165	0.056		
area	1	1.021	0.326		
nutrient level	2	1.225	0.317		r^2adj=0.7184
abundance	**1**	**6.784**	**0.018**	*	

d

abundance, 2012	Df	F	p		
flood	**1**	**14.09**	**0.001**	**	
mowing	2	0.58	0.567		
nectar	**1**	**33.07**	**< 0.001**	***	
area	**1**	**5.44**	**0.031**	*	r^2adj=0.759
nutrient level	2	1.20	0.324		

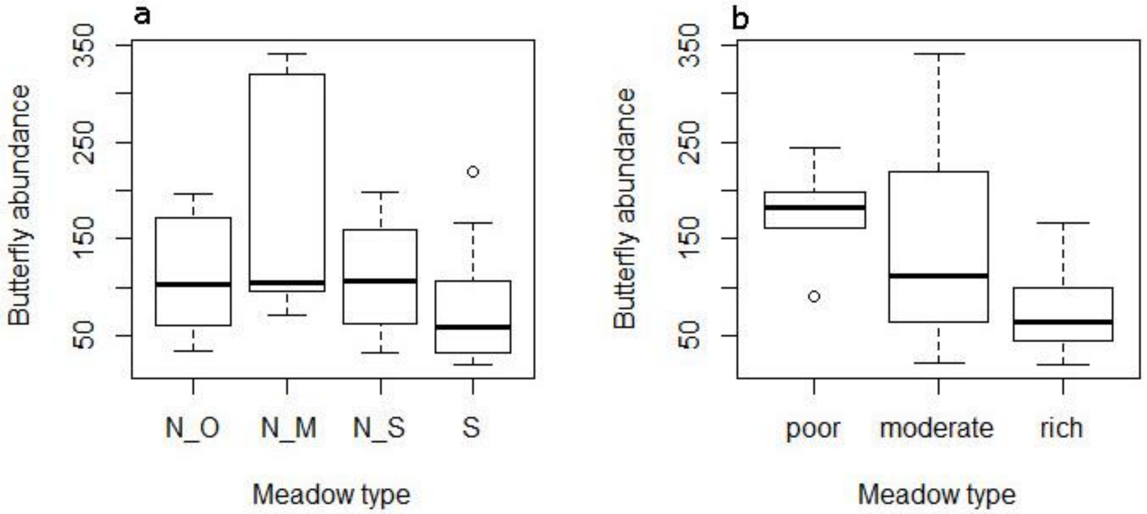

Fig. 4: Overall butterfly abundance relative to (a) flood regime and (b) nutrient status of meadows in the 2013 survey. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: N_O = non flooded with high level of groundwater, N_M = non flooded, N_S = non flooded with flood impact only in 2013, S = annually flooded. Rich = nutrient rich, moderate = moderate nutrient level, poor = nutrient poor.

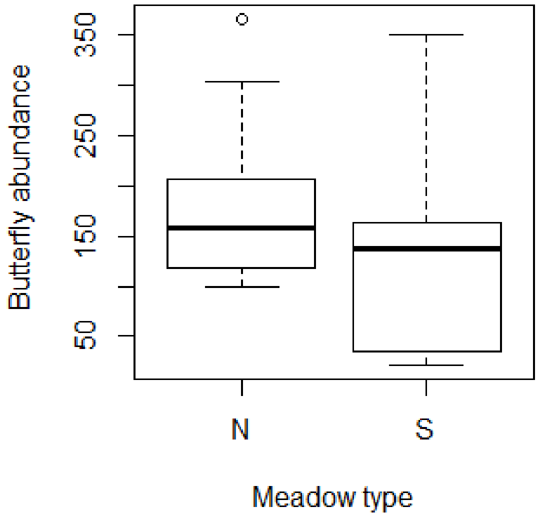

Fig. 5: Overall butterfly abundance relative to flood regime in the 2012 survey. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: N = non flooded, S = annually flooded.

Functional guilds according to larval host use

Table 3 shows the GLM results for the effects of several predictors on the proportional contribution of various feeding guilds to the butterflies sighted per meadow. These guilds comprised species whose caterpillars feed on grass, herbs, woody plants and species of Fabaceae, or of Brassicaceae, respectively. Among all feeding guilds, flooding significantly affected their contribution to local butterfly assemblages (Table 3), but in contrasting ways (Fig. 6). The grass-feeding guild decreased in prevalence in response to flooding of meadows. Meadows less impacted by inundation (N_O, N_M) showed a higher proportion of grass-feeders (Fig. 6a). A similar trend was observed with regard to Fabaceae-feeding species (Fig. 6c). Conversely, the fraction of herb-feeders increased with stronger flood impact, as well as the subset of Brassicaceae-feeders (Figs. 6b, 6d). The nutrient status of meadows only affected the fractions of grass-feeding and herb-feeding species, respectively (Figs. 7a, 7b). Again Brassicaceae-feeders showed a similar trend as the grass-feeding species (Fig. 7c). The proportional contribution of butterflies with caterpillars feeding on woody plants was clearly higher on flood affected meadows (Fig. 6e). In addition, the proportion of Fabaceae-feeders was positively influenced by nectar availability (β = 0.374).

Table 3. Results of general linear models, testing the effects of several predictors on the proportion of individuals whose larvae develop on (a) grass; (b) herbs; (c) woody plants; (d) Fabaceae; (e) Brassicaceae. Significance codes: '*' p < 0.001; '**' p < 0.01; '*' p < 0.05. Significant effects (p < 0.05) in bold case, n.i. = predictor not included in the final model.**

a

grass	DF	F	p	
flood	**3**	**6.22**	**0.002**	**
mowing	2	2.61	0.090	.
nutrient level	**2**	**4.94**	**0.014**	*
nectar	n.i.			

r²adj=0.565

b

herbs	Df	F	p	
flood	**3**	**9.76**	**< 0.001**	***
mowing	n.i.			
nutrient level	**2**	**4.83**	**0.015**	**
nectar	n.i.			

r²adj=0.541

c

woody plants	Df	F	p	
flood	**3**	**3.58**	**0.024**	*
mowing	n.i.			
nutrient level	n.i.			
nectar	n.i.			

r²adj=0.173

d

Fabaceae	Df	F	p	
flood	**3**	**4.26**	**0.013**	*
mowing	n.i.			
nutrient level	n.i.			
nectar	**1**	**6.66**	**0.015**	*

r²adj=0.306

e

Brassicaceae	Df	F	p	
flood	**3**	**2.09**	**0.005**	**
mowing	n.i.			
nutrient level	**2**	**5.21**	**0.013**	*
nectar	1	1.79	0.143	

r²adj=0.496

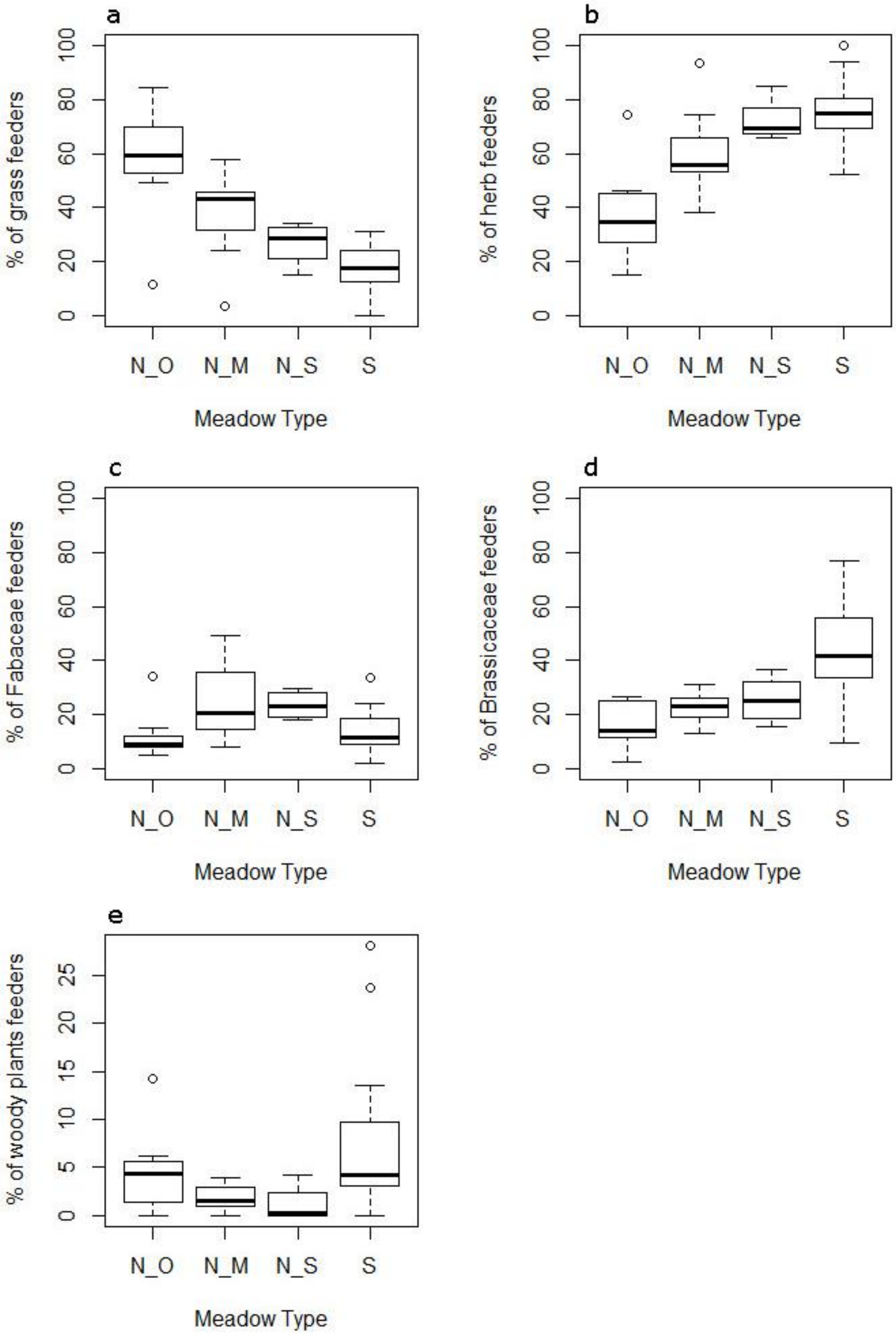

Fig. 6: Proportional contribution of (a) grass-feeding individuals, (b) herb-feeding individuals, (c) Fabaceae-feeding individuals, (d) Brassicaceae-feeding individuals and (e) woody plants feeding individuals relative to flood regime. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: N_O = non flooded with high level of groundwater, N_M = non flooded N_S = non flooded with flood impact only in 2013, S = regularly flooded.

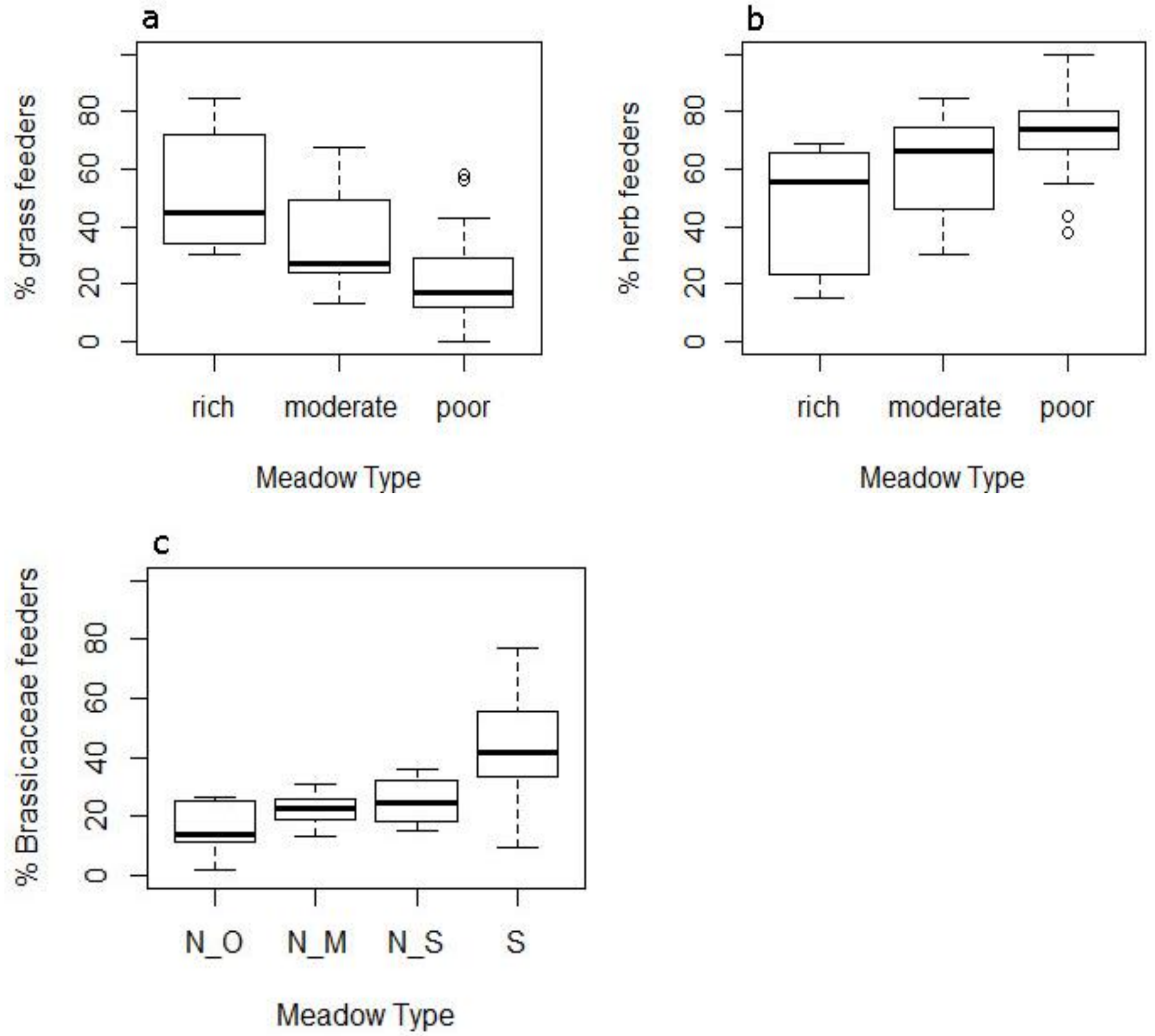

Fig. 7: Proportional contribution of (a) grass-feeding individuals, (b) herb-feeding individuals and (c) Brassicaceae-feeding individuals relative to nutrient level. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: rich = nutrient rich, moderate = moderate nutrient level, poor = nutrient poor.

Butterfly groups according to habitat preferences

Butterfly groups defined by habitat preferences (species that predominantly inhabit meadows, meadow margins, and forest margins, respectively) were differentially represented according to the nutrient status of the meadow sites, whereas no pattern emerged with regard to flood regime (Table 4). True meadow species were more frequently found on nutrient poor sites (Fig. 8a), whereas forest margin and woodland species were relatively more common on nutrient rich sites (Fig. 8b, c).

Table 4. Results of general linear models, testing the effects of several predictors on the percentage of individuals representing (a) meadow species, (b) meadow margin species and (c) woodland species. Significance codes: '*' p < 0.001; '**' p < 0.01; '*' p < 0.05. Significant effects (p < 0.05) in bold case, n.i. = predictor not included in the final model.**

a

meadow	Df	F	p	
flood	3	2.83	0.054	.
mowing	n.i.			
nutrient level	**2**	**6.15**	**0.006**	**
nectar	1	2.27	0.142	

r²adj=0.362

c

forest margin	Df	F	p	
flood	n.i.			
mowing	n.i.			
nutrient level	**2**	**4.05**	**0.026**	*
nectar	n.i.			

r²adj=0.141

b

meadow margin	Df	F	p	
flood	n.i.			
mowing	2	2.32	0.114	
nutrient level	**2**	**10.47**	**< 0.001**	***
nectar	n.i.			

r²adj=0.401

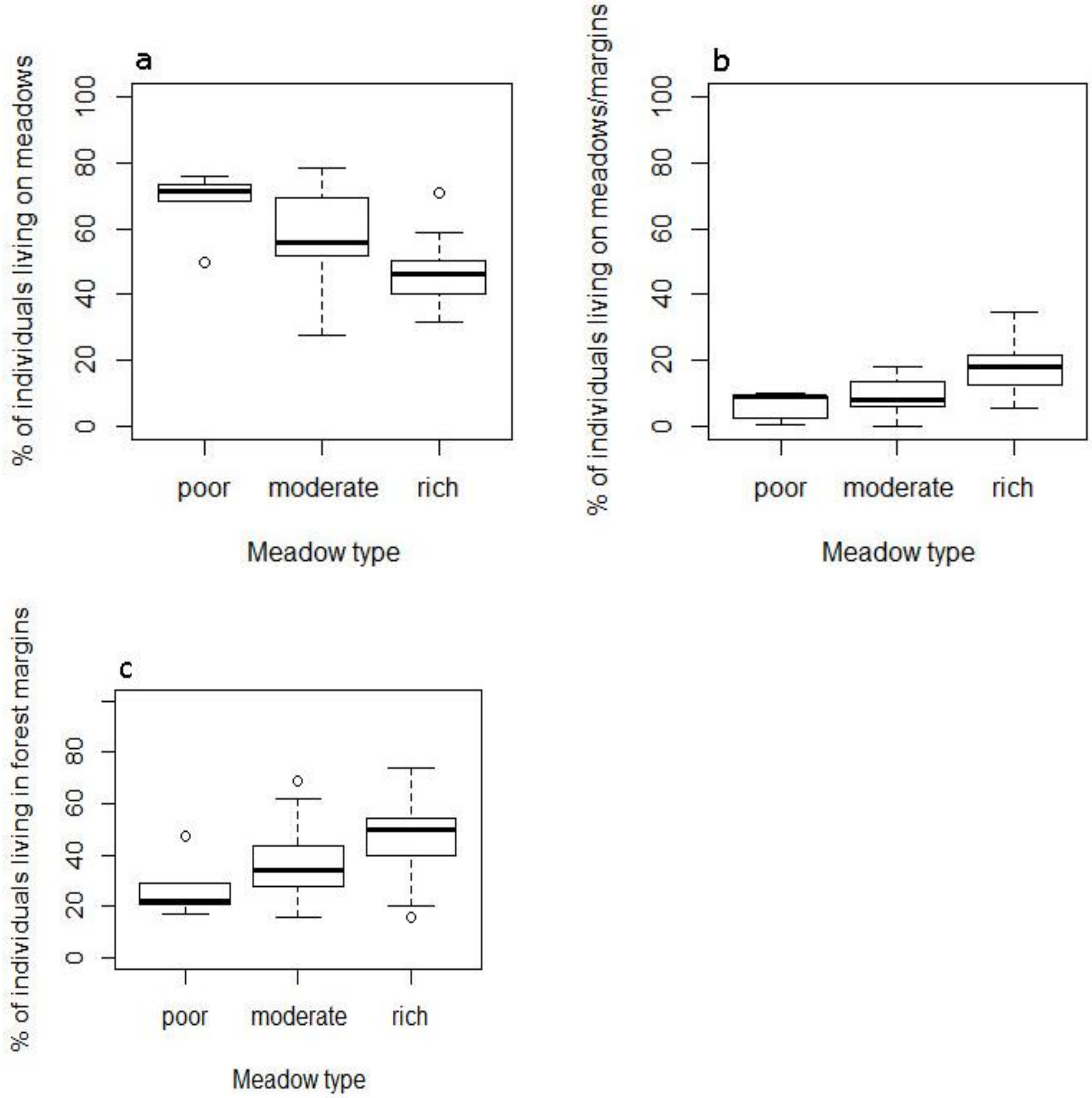

Fig. 8. Proportional contribution of (a) individuals living on meadows, (b) individuals living on meadow margins and (c) individuals living in forest margins relative to nutrient level. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: rich = nutrient rich, moderate = moderate nutrient level, poor = nutrient poor.

Functional groups according to adult life-history traits and climatic niche dimensions

The percentage of individuals representing butterfly species with very high fecundity (Table 5) differed significantly between flood regimes. Low fecundity butterflies were less prevalent on the southern meadows, whereas species with very high fecundity were relatively more common there (Fig. 9).

Table 5. Results of the general linear model, testing the effects of several predictors on the percentage of the relative representation of individuals with very high fecundity. Significance codes: '*' $p < 0.05$. Significant effects ($p < 0.05$) in bold case, n.i. = predictor not included in the final model.

very fecund	Df	F	p	
flood	**3**	**4.45**	**0.011**	*
mowing	2	1.77	0.188	
nutritient level	2	0.35	0.706	
nectar	1	1.26	0.270	

r^2adj= 0.339

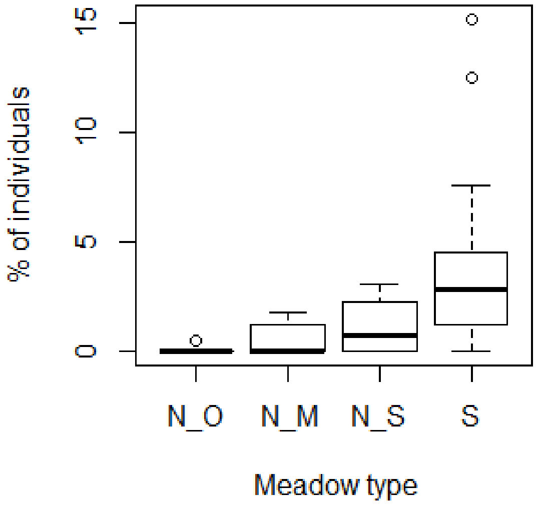

Fig. 9. Relative representation of butterflies with very high fecundity relative to flood regime. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: N_O = non flooded with high level of groundwater, N_M = non flooded, N_S = non flooded with flood impact only in 2013, S = regularly flooded.

Truly migratory (Table 6a) and highly dispersive, but non-migratory butterflies (Table 6b) were more common on flood-prone meadows (Figs. 10a, 10b), whereas individuals that show strong side fidelity (Table 6c) decreased with flood impact (Fig. 10c). These territorial butterflies were also distinctly more common on nutrient rich meadows (Fig. 10d).

Table 6. Results of general linear models, testing the effects of several predictors on the percentage of the relative representation of (a) migratory, (b) dispersive individuals and (c) individuals showing strong side fidelity. Significance codes: '*' p < 0.001; '**' p < 0.01; '*' p < 0.05. Significant effects (p < 0.05) in bold case, n.i. = predictor not included in the final model.**

a

migratory	Df	F	p	
flood	**3**	**3.48**	**0.026**	*****
mowing	n.i.			
nutrient level	n.i.			

r^2adj= 0.167

b

dispersive	Df	F	p	
flood	**3**	**11.52**	**< 0.001**	*******
mowing	2	2.52	0.097	.
nutrient level	2	1.83	0.177	

r^2adj= 0.66

c

side fidelity	Df	F	p
flood	**3**	**7.30**	**< 0.001**
mowing	n.i.		
nutient level	**2**	**9.31**	**< 0.001**

r^2adj= 0.586

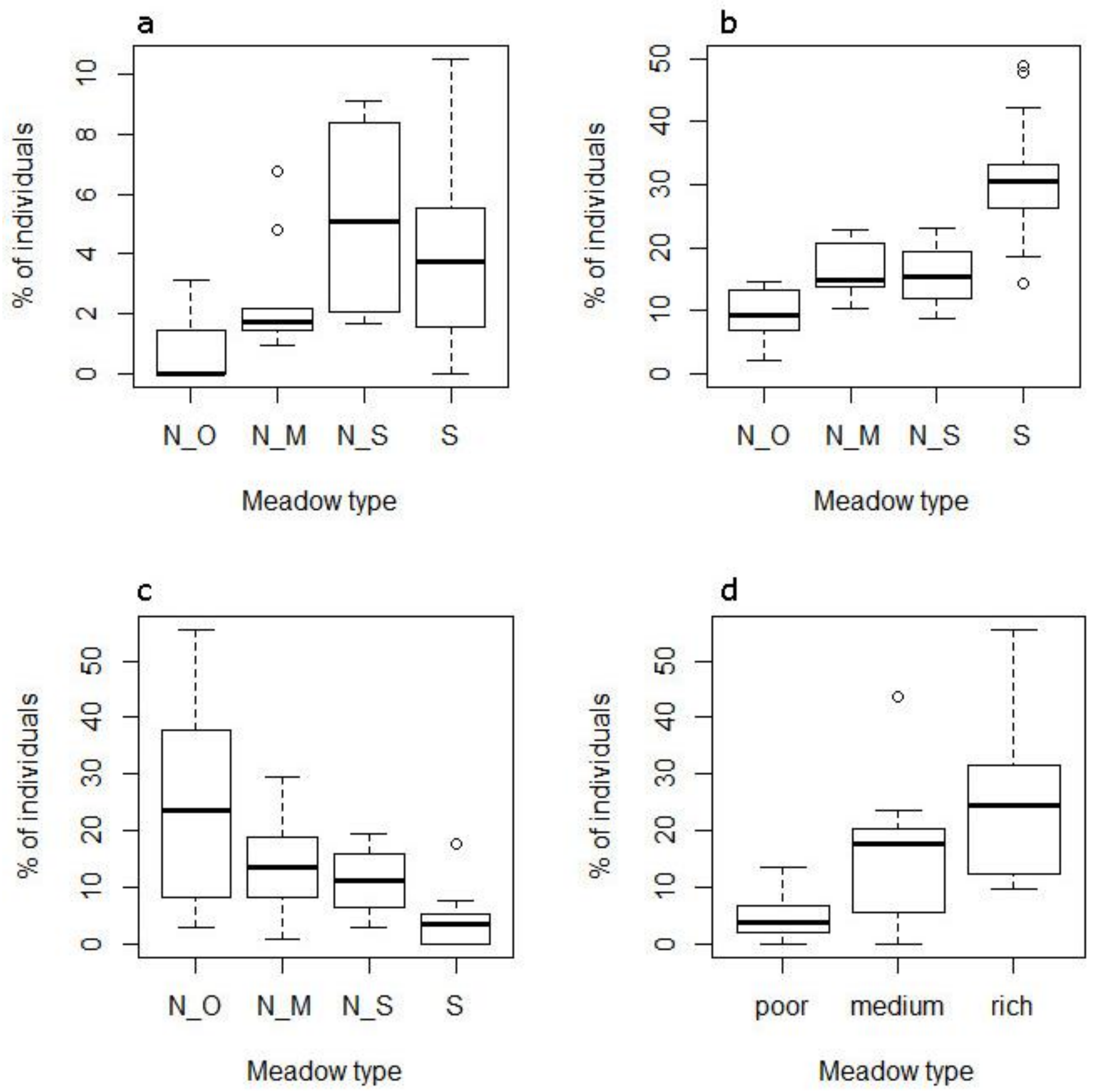

Fig. 10. Relative representation of (a) migratory, (b) dispersive individuals, (c) butterflies showing strong side fidelity relative to flood regime and (d) butterflies showing strong side fidelity relative to nutrient level. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: N_O = non flooded with high level of groundwater, N_M = non flooded meadows, N_S = non flooded with flood impact only in 2013, S = regularly flooded. Rich = nutrient rich, moderate = moderate nutrient level, poor = nutrient poor.

Butterflies with a very long lifespan were slightly more common on meadows with the highest flood impact and were least common on meadows near Orth (Table 7, Fig. 11). The proportions of uni- and polyvoltine butterflies showed no significant influence of any of the predictors tested.

Table 7. Results of general linear model, testing the effects of several predictors on the percentage of the relative representation of individuals with a very long lifespan. Significance codes: p < 0.05. Significant effects (p < 0.05) in bold case, n.i. = predictor not included in the final model.

long lifespan	Df	F	p	
flood	**3**	**3.98**	**0.016**	*
mowing	n.i.			
nutrient level	n.i.			
nectar	n.i.			

r^2adj= 0.195

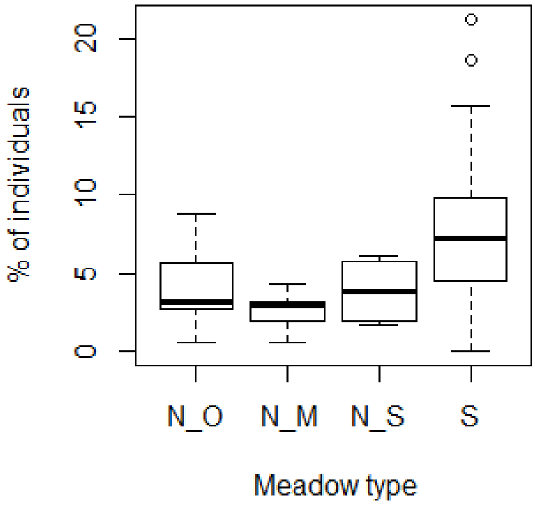

Fig. 11. Relative representation of butterflies with a very long lifespan relative to flood regime. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: N_O = non flooded with high level of groundwater, N_M = non flooded, N_S = non flooded with flood impact only in 2013, S = regularly flooded.

The Community Precipitation Index (i.e. abundance-weighted average of Species Precipitation Index values) was significantly highest on the northern meadows near Orth (N_O), followed by the southern meadows (Table 8, Fig. 12). However, differences were small relative to the large variance between butterfly assemblages. Neither the Community Temperature Index nor the Community Soil Moisture Index showed any significant relationship with the tested predictors.

Table 8. Results of general linear model, testing the effects of several predictors on the Community Precipitation Index of butterfly assemblages. Significance codes: p < 0.05. Significant effects (p < 0.05) in bold case, n.i. = predictor not included in the final model.

perciptation	Df	F	p-value	
flood	**3**	**3.42**	**0.028**	*
mowing	n.i.			

r^2adj=0.164

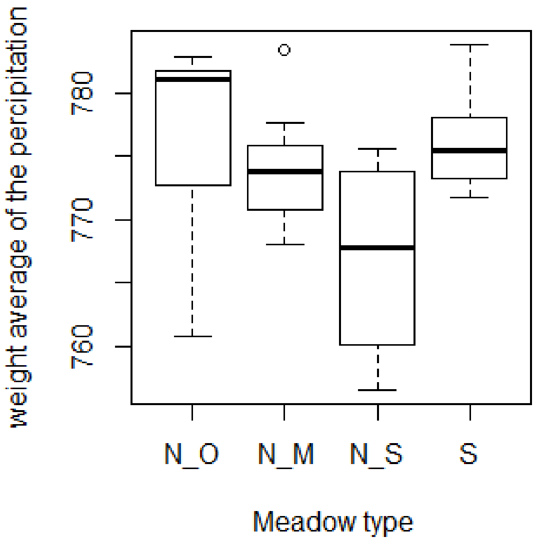

Fig. 12. Community precipitation index of butterfly assemblages relative to flood regime. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: N_O = non flooded with high level of groundwater, N_M = non flooded, N_S = non flooded with flood impact only in 2013, S = regularly flooded.

Species composition

Figs. 13 and 14 show NMDS ordinations of butterfly communities, based on Bray-Curtis similarities, including relationships with environmental predictors fitted into the diagrams as vectors (Table 9). The end points of the vectors are Spearman rank correlation coefficients between ordination axis scores of the communities and the respective predictors (Table 10). In both years butterfly species composition differed prominently between non-flooded meadows (north of the levee, blue symbols) and flooded meadows (south of the levee, red symbols). This is also indicated by the flood vectors, which reflect the largest fraction of explained variance in species composition. In 2013 the nutrient status of meadows also contributed strongly to separating butterfly communities, with more nutrient-rich meadows often being associated with stronger flooding impact (Fig. 13). The impact of mowing influenced species composition only, and rather weakly, in the year 2012 (Fig. 14). The role of a meadow's nectar sources on butterfly species composition was slightly stronger in 2012 (r^2 = 0.123) than in 2013 (r^2 = 0.073). High nectar availability was usually associated with low flood impact.

Table 9. Results of a Multivariate Analysis of Variance of the Bray-Curtis similarity matrix, using a permutation test with pseudo F-ratios. The predictors NMDS1 and NMDS2 are the two ordination axis scores of the plant species community (presence/absence). Significance codes: '*' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$. Significant effects ($p < 0.05$) in bold case.**

2013	Df	F	r^2	p	
flood	**3**	**4.012**	**0.230**	**0.001**	***
nutrient level	**2**	**2.383**	**0.091**	**0.004**	**
nectar	**1**	**3.817**	**0.073**	**0.002**	**
mowing	2	1.214	0.046	0.241	
area	1	1.566	0.030	0.103	
NMDS1	1	1.749	0.033	0.071	
NMDS2	1	0.921	0.018	0.495	

2012	Df	F	r^2	p	
flood	**1**	**5.754**	**0.159**	**0.001**	***
nutrient level	2	0.936	0.052	0.543	
nectar	**1**	**4.437**	**0.123**	**0.001**	***
mowing	**1**	**2.409**	**0.064**	**0.018**	*
area	1	1.828	0.051	0.064	
NMDS1	1	1.665	0.046	0.112	
NMDS2	1	1.134	0.031	0.294	

Table 10. Spearman rank correlation coefficients between NMDS axis scores of butterfly assemblages (X, Y) and environmental descriptors of the meadows for 2013 and 2012 surveys. Significant effects ($p < 0.05$) in bold case.

2013	X	Y	2012	X	Y	
flood	**0.4240**	**0.6543**	**habitat**	**0.8089**	**0.0951**	**
nectar	-0.4118	0.2188	nectar	-0.3268	-0.0003	
nutrition	-0.5227	-0.2630	mowing	-0.3480	0.3480	

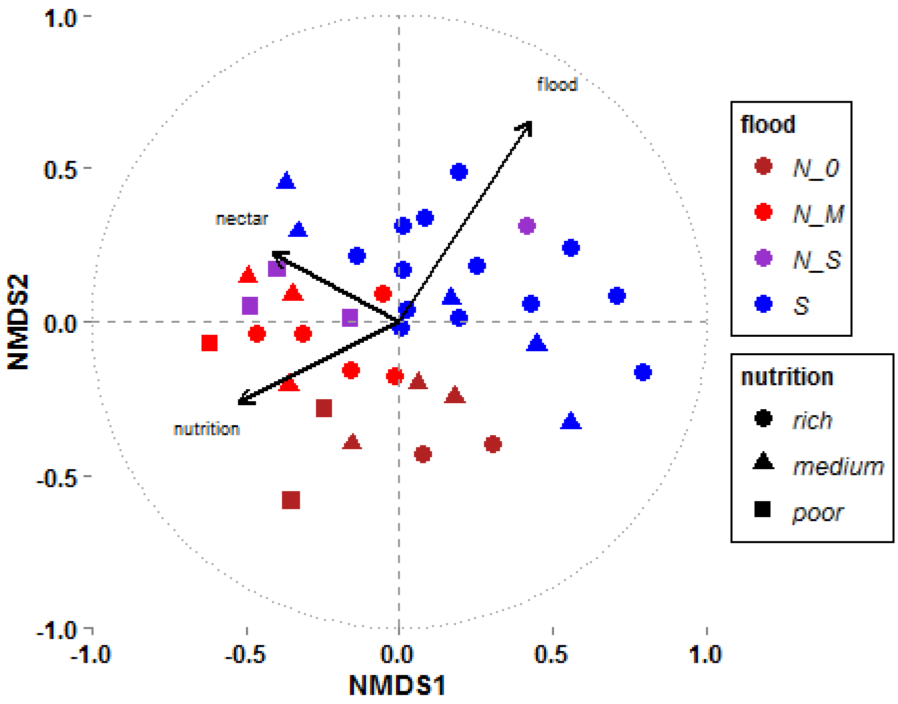

Fig. 13. NMDS based on Bray-Curtis similarity of 2013 butterfly communities; vectors fitted into the ordination calculated as Spearman's rank correlation coefficients between ordination axis scores of the communities and the respective predictor values. Stress = 0.2329.

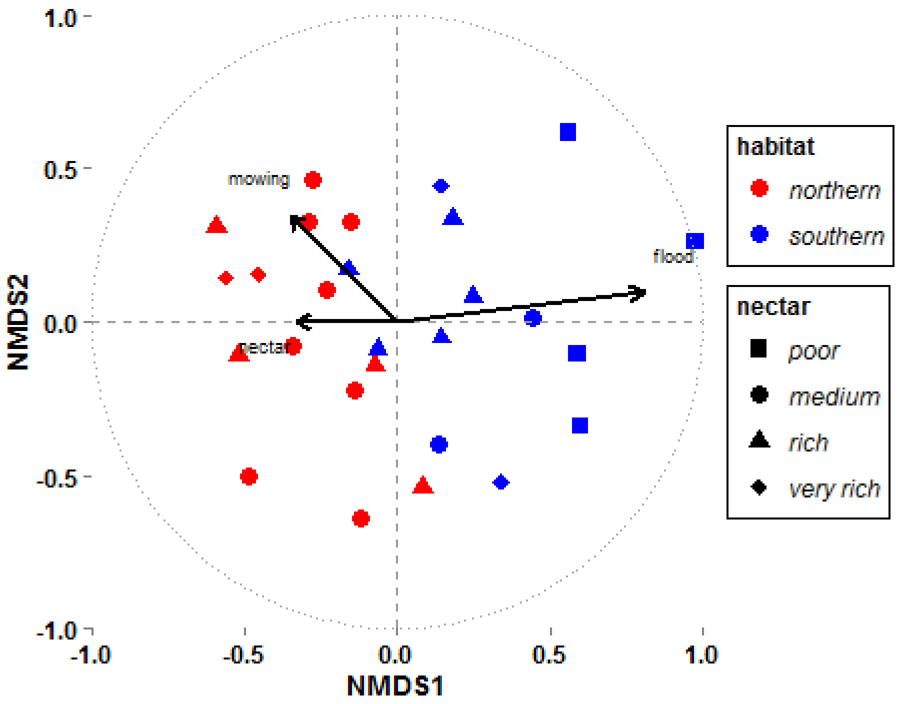

Fig. 14. NMDS based on Bray-Curtis similarity of 2012 butterfly communities; vectors fitted into the ordination calculated as Spearman's rank correlation coefficients between ordination axis scores of the communities and the respective predictor values. Stress = 0.1929.

Fig. 15 shows an NMDS ordination of the combined survey data from the years 2012 and 2013. Butterfly communities of the northern meadows showed a far smaller multivariate dispersion in 2012 than in exceptional flood year 2013, when also many of these meadows became inundated. The southern meadows prone to annual floods, in contrast, exhibited a rather similar degree of multivariate dispersion of their butterfly assemblages. Overall, segregation of butterfly communities due to flooding was reflected along the first ordination axis, whereas differences between years were related to the second ordination axis. ANOSIM testing for differences in species composition revealed significant differences between the northern part and the southern part of the Nationalpark, as well as the years 2012 and 2013 (Table 11).

Table 11. Results of analysis of similarities (ANOSIM), testing for differences in species composition of the northern, not flooded meadows and the southern, flooded meadows and the years 2012 and 2013.

	R	p
north vs. south	0.3321	0.001
2012 vs. 2013	0.2525	0.001

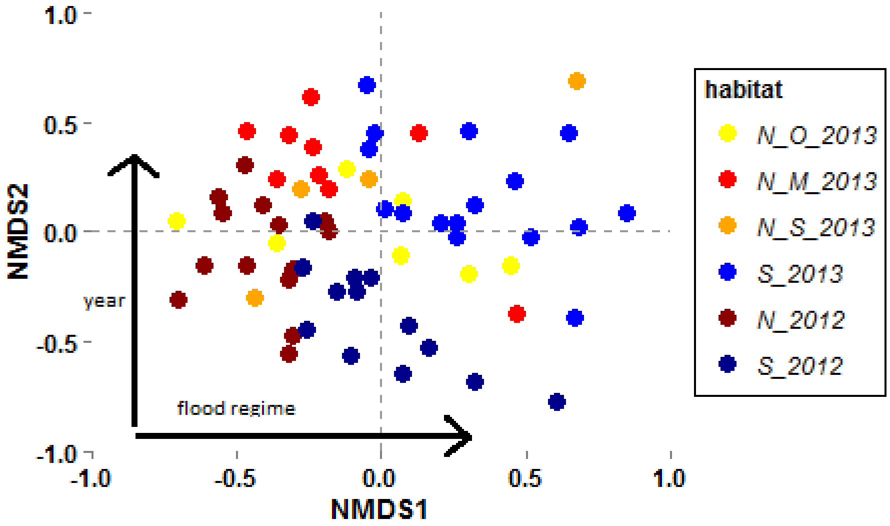

Fig. 15. NMDS plot based on Bray-Curtis similarities of the 2012 and 2013 butterfly surveys combined, Stress= 0.2363.

Figs. 16a and 17a show the average abundances of those species which were collectively responsible for 80% of the differences in species composition between the northern and southern meadows in 2013 (Fig. 16a) and 2012 (Fig. 17a). In the 2013 survey 13 and in the 2012 survey 12 species contributed to the 80% of the differences in the species composition, whereas the first nine species are exactly the same (Figs. 16a, 17a). In Figs. 16b and 17b the proportional contribution of the species to the community dissimilarity are illustrated.

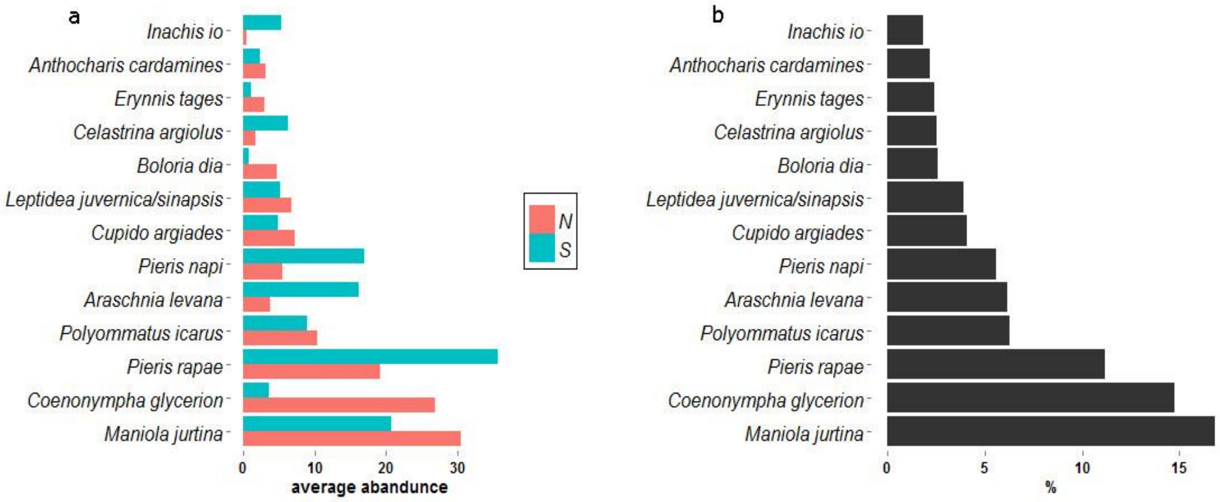

Fig. 16. (a) Average abundance of the 13 species responsible for 80% discrimination in butterfly species composition (Bray-Curtis dissimilarity) between the northern and southern meadows, according to the SIMPER algorithm in 2013, (b) percentage contribution of these species to discrimination between northern and southern meadows in 2013.

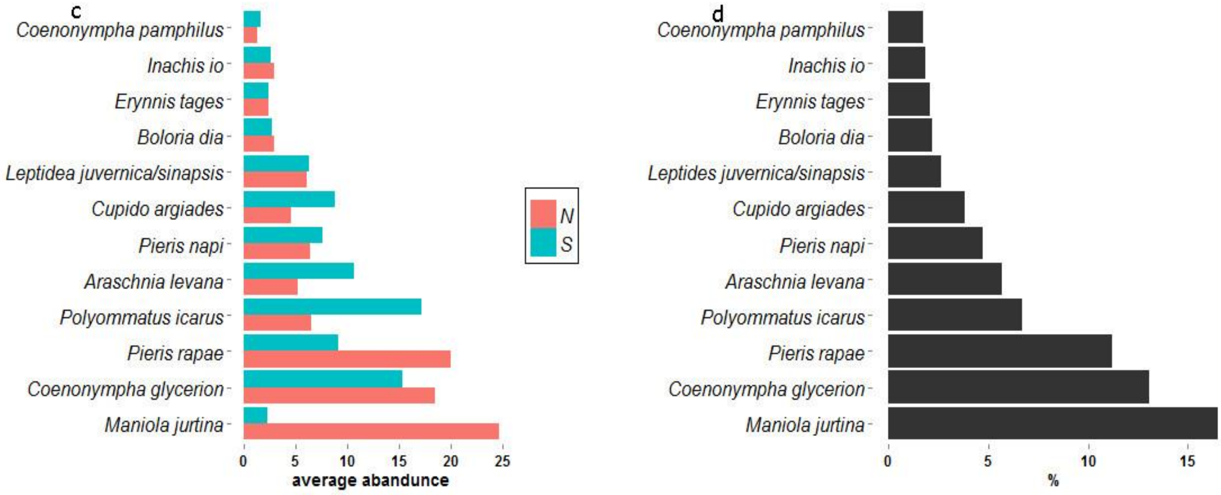

Fig. 17 (a) Average abundance of the 12 species responsible for 80% discrimination in butterfly species composition (Bray-Curtis dissimilarity) between the northern and southern meadows, according to the SIMPER algorithm in 2012, (b) percentage contribution of these species to discrimination between northern and southern meadows in 2012.

Functional Diversity

The Functional Evenness Index (FEve) was significantly highest on the southern meadows (S), and the northern meadows near Orth (N_O) (Table 12b, Fig. 18). In addition, Functional Evenness was negatively affected by area ($\beta = -0.462$). The Functional Divergence Index (FDiv) was significantly highest on the meadows near Orth (N_O), followed by the southern meadows (S) (Table 12c, Fig. 18). Functional Richness showed no significant influence by any of the tested factors (Table 12a).

Table 12. Results of general linear models, testing the effects of several meadow characteristics on (a) Functional Richness (FRic), (b) Functional Evenness (FEve) and (c) Functional Divergence (FDiv) of butterfly assemblages. Significance codes: '' p < 0.01; '*' p < 0.05. Significant effects (p < 0.05) in bold case, n.i. = predictor not included in the final model.**

a

Fric	Df	F	p	
flood				
mowing	2	2.74	0.079	.
nectar	1	2.50	0.123	
nutrient level	n.i.			
area	n.i.			

r^2adj=0.120

b

FEve	Df	F	p	
flood	**3**	**3.17**	**0.038**	*
mowing	2	1.82	0.179	
nectar	n.i.			
nutrient level	n.i.			
area	**1**	**8.26**	**0.007**	**

r^2adj=0.200

c

FDiv	Df	F	p	
flood	**3**	**3.28**	**0.033**	*
mowing	2	2.87	0.071	.
nectar	n.i.			
nutrient level	n.i.			
area	n.i.			

r^2adj=0.181

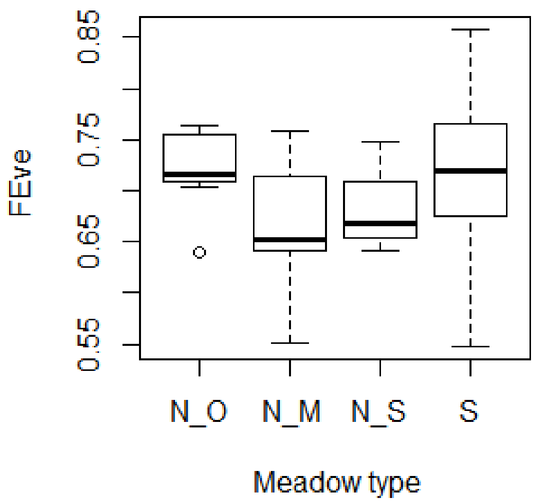

Fig. 18. Functional Evenness Index (FEve) relative to flood regime. Box-and-whisker-plot, range= 1.5 * IQR. Meadow types: N_O = non flooded with high level of groundwater, N_M = non flooded, N_S = non flooded with flood impact only in 2013, S = regularly flooded.

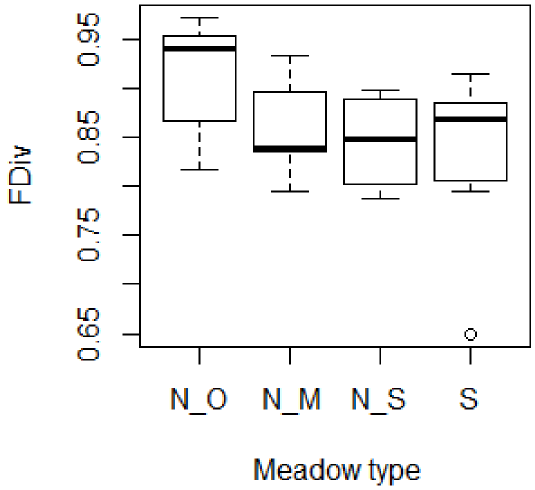

Figure 19. Functional Divergence Index (FDiv) relative to flood regime. Box-and-whisker-plot, range = 1.5 * IQR. Meadow types: N_O = non flooded with high level of groundwater, N_M = non flooded, N_S = non flooded with flood impact only in 2013, S = regularly flooded.

Discussion

Local butterfly richness, abundance and survey coverage

On the northern meadows in 2013, 63 of the 82 expected species were found. Species accumulation analysis pointed out that approximately ten rare species were still missing in my surveys. On the one hand this leads to the conclusion that still not enough meadows were sampled to cover all rare species. On the other hand, four of the missing species might just have been those which were seen once in the southern part: *Satyrium w-album*, *Polyommatus semiargus*, *Argynnis aglaia* (has been seen twice) and *Melitaea aurelia*. *P. semiargus* and *M. aurelia* were indeed found once on a northern meadow in 2012, underlining the possibility that these species may be two of the rare species missing on the northern meadows in the 2013 survey. Also *Neozephyrus quercus*, *Thecla betulae* and *Satyrium pruni,* which were not found on the northern part in the 2013, but in the 2012 survey, might belong to this set of missing species. Even though they are classified as endangered on the Red List of Lower Austria (HÖTTINGER & PENNERSTORFER 1999 cit. in HÖTTINGER *et al.* 2013), their host plants were all more or less frequently found in the floodplain forests surrounding the northern meadows. Additionally, *N. quercus, S. w-album*, *S. pruni*, *T. betulae* and *A. aglaja* might just have been overlooked because they inhabit forest margins and are not seen on meadows very often. Finally, also *Melitaea diamina* and *Lasiommata megera,* which were both reported once on a southern meadow in earlier study years, might contribute to the missing species on the northern meadows of the 2013 survey. Hence, it is quite likely that all species suspected to be overlooked in these surveys had indeed been observed either on the flood-prone meadows or in earlier years in the region. In contrast to the northern meadows, the number of sampled southern meadows was completely sufficient in the 2013 survey.

After analysing all three sampling years together, an estimated number of 11 rare butterfly species was still missing for the northern part of the National Park. Species accumulation curves for the southern meadows of all three sampling periods were more saturated than the northern ones, with only six rare species missing. As expected, the southern meadows therefore reveal a smaller number of species from the regional species pool because the flooding impact acts as a filter, reducing the abundance and concomitantly the species number.

In the Viennese part of the National Park (the so-called Lobau) additionally 12 species were reported thus far (Table 14) (HÖTTINGER *et al.* 2013). Seven of these (*Cacharodus alceae*, *Spialia sertorius*, *Glaucopsyche alexis*, *Polyommatus amandus*, *Polyommatus bellargus*, *Erebia medusa* and *Melitaea phoebe*) are xerothermophilous and hence are supposed to be rather found on the northern meadows near Orth, if at all. Indeed, some of these (such as *M. phoebe*) have been observed on dry habitats along the Marchfeld levee near Orth and their occurrence on at least some of the northern meadows is hence very probable. The remaining four species might also contribute to the missing species on the southern meadows (*Callophrys rubi*, *Melitaea athalia*, *Lasiommata maera* and *Nymphalis antiopa*). In summary, butterfly species missed during the surveys in the Orth surroundings between 2005 and 2013 in all likelihood would largely belong to the species pool already noted for the adjacent Lobau area.

Altogether the 2013 survey, conducted over a whole vegetation period, reported 64 species (77 %) out of the 83 expected species (Table 14). In comparison, samplings of the 2012 survey, which were only done in June and July and on fewer sampling sites, revealed 53 species (64% of the expected species). The 2005 survey, which was done in May and June and on the smallest number of sampling sites, produced only 40 species (48% of the expected species pool). Taken together, the surveys aggregated over three years discovered 72 species (87% of the known species pool), thus only little more than in the 2013 survey alone. Therefore, if sampling is done during one whole season this would suffice to get a near-complete species list. In relative terms, butterfly sampling exclusively in June and July might be sufficient, covering only 13% of the species less for the least effort. Phenologically only two species might not be found on the wing during this period, viz. *Anthocharis cardamines* and *Zerynthia polyxena*. In the Nationalpark Donau-Auen a partial second generation of *C. rubi* may be found until September. The first generation of this species only flies until the beginning of June. Also *G. alexis* was proven to be found until October for eastern Austria (HÖTTINGER *et al.* 2013).

Generally speaking, more species were found on meadows with more individuals. Even though species accumulation curves indicate the local species richness on the flooded southern meadows to be smaller than on the not flooded northern meadows, no significant influence of the flooding regime on the number of detected species per sites could be shown by regression analysis. However, butterfly abundance was significantly highest on meadows without any flooding impact (N_M), which was also the case in 2012, i.e. a year with less flooding impact. It can therefore be concluded that the southern meadows reveal a lower number of species from the regional species pool, because the flooding reduces the abundance and consequently the species number. A smaller number of species and abundance was also found for spiders and bugs due to longer flooding durations (BONN *et al.* 2002, GRATZER *et al.* 2012), whereas the number of identified moth species and abundance was similar at flooded and not flooded meadows (TRUXA & FIEDLER 2012). Additionally meadows with a lower nutrient level harboured more butterfly individuals. This result might directly be linked to the flood regime, as most of the northern meadows are also nutrient poor. Also flower nectar availability influenced the abundance positively, especially if the flood intensity was less (as in 2012). Nectar resource limitation of butterfly abundance has been proven in several studies on different butterfly species and communities (BOGGS 1987, HOLL 1995, SCHULTZ & DLUGOSCH 1999, CROXTON *et al.* 2005, SAARINEN *et al.* 2005). Many butterflies achieve a longer lifespan and higher fecundity, as nectar availability increases (HILL 1992, BOGGS & ROSS 1993, SCHULTZ & DLUGOSCH 1999). It has also been proven that the microdistribution of butterflies is influenced by the flower nectar resource of the different patches in a mosaic-like habitat. Butterflies accumulate in patches that are flower rich (LOERTSCHER *et al.* 1995). In general, one may conclude that nectar resources become the most important limiting factor of butterfly abundance on the meadows in the study area, when flooding is less intense. These findings also indicate that the differences in the local species richness in 2013 might be caused indirectly by flower nectar availability. As generally more species were found, where more individuals were sighted and the meadows with a higher flower nectar availability harboured more individuals.

Butterfly species composition

Flooding emerged as the crucial factor altering butterfly species composition on the meadows in the area, presumably acting on the immobile egg, larval and pupal stages. Also TRUXA & FIEDLER (2012) observed strong differences in species composition of moths relative to the flood regime along three riverine floodplains in Eastern Austria. A major influence of inundation on species composition of carabid beetle assemblages was found along several large rivers in Germany (BONN *et al.* 2002, GERISCH *et al.* 2006) and on bug communities at the Morava river (GRATZER *et al.* 2012). This results stand in contrast to the general findings of BONN *et al.* (2002), who found rather the habitat structure to alter spider species composition than the flooding regime per se. Fitting to the findings of TRUXA & FIEDLER on moth (2012) and VAN HELSDINGEN (1997) on spider communities, but in contrast to previous expectations, no characteristic floodplain meadow butterfly community, consisting of species specific to humid habitats, was found. Almost one half of the difference in species composition between the northern and southern meadows was explained by abundance differences of the three most abundant ubiquitous species, *Maniola jurtina* (16.8% of between-habitat differentiation), *Coenonympha glycerion* (14.7%) (both more frequent on the northern meadows) and *Pieris rapae* (11.2%, more abundant on the southern meadows). The first two species are grass-feeders. Representatives of this feeding guild were generally proven to be more frequent on the meadows with no or little flooding impact (N_M, N_O). In total only 13 butterfly species contributed 80% to the difference in species composition relative to flood impacts. Of these, only *Araschina levana* with 6.1% contribution may be described as typical floodplain forest species. Species that were limited or more common on the northern meadows were mostly species inhabiting dry and warm habitats like *Hesperia comma, Polyommatus coridon, Plebejus argus* and *Plebejus arygnomon.* But even if *P. argus* and *P. arygnomon* were sighted pretty frequently on the northern meadows, these species did not influence the different species composition of the northern and southern meadows considerably. Also *Aphantopus hyperantus* was only seen on the northern meadows, though with 29 individuals contributing only 0.96 % to the difference in species composition. A possible explanation for this preference for non-flooded sites is found in its egg-laying habits. *A. hyperantus* females merely drop their eggs to the ground without any attachment, making them more easily being drifted away (WIKLUND 1984, EBERT 1993). All the same, the eggs of *Melangaria galathea* are drifted away. This species was sighted more often on the northern meadow (18 individuals), than on the southern meadows (4 individuals). Also the eggs of this species are just dropped to the ground, while the female is sitting on a blade of grass. Moreover no sticky exudate, fixing the eggs could be found for this species (SONNTAG 1981, EBERT 1993).

The second factor modifying butterfly species composition in the 2013 survey was the nutrient level of the meadows. The average nutrient level of a meadow may be seen as indicator for the availability of the host plants, hence also acting on the immobile larval stages of the butterfly's life cycle. As already mentioned, the nutrient level is strongly linked to the flood regime, as most of the flooded meadows are also nutrient rich. Generally, xerothermophilous butterfly species, inhabiting dry and warm meadows suffer from the eutrophication which happens on the southern meadows not only because their host plants might be missing. They might also not be capable to finish their lifecycle because of colder microhabitats caused by taller perennial herbs (THOMAS & JONES 1993, MAES & VAN DYCK 2001). Therefore xerothermophilous grass land species contribute rather to the species composition on the northern sides and only on the less nutrient rich southern meadows. The guild of the butterflies, inhabiting meadow margins and forest margins definitely benefit of the higher perennial herbs on the meadows with higher nutrient level. Also regression analysis revealed true meadow species to be more common on nutrient poor sites, whereas forest margins or even woodland species were more frequently spotted on the nutrient rich meadows.

Also the mowing exclusively altering the species composition in the 2012 survey, as described below, acts on the immobile larval stages.

Only at third rank butterfly species composition in both years was influenced by the availability of nectar, which is resource class acting on the adult stages.

Against expectations, the axis scores of the NMDS of the species plant list did not reveal any significant influence on the species composition. Even if the species list only revealed absence and presence data, a marginal influence of this predictor on the species composition was expected, as many butterflies are limited to only a few plant taxa as larval host plants. Obviously the abiotic factors analysed (flood, nutrient level, mowing and nectar) dominated the influence of the biotic interaction viz. the host plant availability, on the butterfly species composition. Supporting our expectations, many studies revealed the host plant availability to be an important factor acting on the distribution and stability of butterfly populations (i.e. SHAHABUDDIN *et al.* 2000, THOMAS *et al.* 2001, SHAPIRO 2002, KOH *et al.* 2004). Especially for monophagous butterflies like *P. coridon* and *Cupido minimus*, which were also found at the surveys of this work, host plant density was shown to be the most important predictor for occurrence and population density (KRAUSS *et al.* 2004, KRAUSS *et al.* 2005). Low host plant density or absence was even shown to be the main factors driving butterfly species to extinction (THOMAS 1983, WAHLBERG *et al.* 2002, LEÓN-CORTÉS *et al.* 2003, HULA *et al.* 2004, KRAUSS *et al.* 2005).

Differences with regard to feeding guilds and functional groups

Even though meadow butterfly communities did not differ starkly with regard to their species richness between flooding regimes, species composition was very strongly shaped by the incidence of annual summer floods. These differences in compositional diversity translated further into variation at the guild or functional group level. I found a higher percentage of individuals feeding on herbs, and especially of Brassicaceae feeders, on the southern meadows and the northern meadows with the highest flooding impact in 2013 (N_S). All Brassicaceae feeders were members of Pieridae; *Anthocharis cardamines, Pieris brassicae, Pieris napi, Pieris rapae* and *Pontia edusa. P. rapae* and *P. napi* were seen very frequently on the southern meadows. Additionally *P. napi* was sighted more often on the southern meadows than on the northern meadows. Both are common ruderal species with at least three flight periods (STETTMER *et al.* 2011) that may easily recolonize the southern meadows after inundation. *P. edusa* was also found more often on the southern meadows. Even if this species inhabits warm and dry habitats, it may also recolonize the southern meadows easily, as the highly migratory imagines may be found on the wing from April to October with up to four generations. In contrast *A. cardamines* does not contribute to the Brassicaceae feeders that are more common on the southern meadows, as it is only univoltine and is exposed to the inundations as pupae or larvae, viz. the most immobile stages. *P. brassicae* was only found twice on the southern side and once on the northern side*,* which is not surprising as this hemerophilous species needs large-sized agricultural planted Brassicaceae*,* because their eggs are laid in large clutches of up to 100 individuals*.* As relatively more Brassicaceae feeders were found on the southern meadows, it may be assumed that more Brassicaceae were growing on the southern side. As only a presence/absence list of plant species was available, this assumption cannot be affirmed. The following can, however, be stated: The Brassicaceae found on the meadows were ruderal species, associated with high Ellenberg indicator values for nitrogen (i.e. *Alliaria* *petiolata*) (Ellenberg *et al.* 1992), indicating these species to benefit of the disturbance caused regularly by the inundations and the high nutrient level of the southern meadows. In general the higher percentage of Brassicaceae-feeders could therefore be an indication that the southern butterfly communities are ruled by eutrophication and ruderalisation like the plant community.

In contrast, the biggest proportion of grass-feeding individuals was found on the meadows near Orth (N_O), which were influenced by uprising groundwater, followed by the meadows with no (N_M) or little flooding impact (N_S). The northern meadows that were only a little bit or not disturbed by the inundation tended to harbour typical grassland butterfly communities. Therefore the more disturbed the meadows were by the flooding regime, the less likely a typical grassland butterfly community was established.

As expected the highest proportion of butterflies whose caterpillars feed on woody plants was found on the flooded meadows, as the larval stages of this guild may not really be affected by most inundation events. Moreover most of the species feeding on woody plants are true floodplain-species (i.e. *Apatura ilia*), adapted to the regular disturbance of inundations. Also arboreal moth were much less affected by the flooding impact than moth species living in the ground-layer (Truxa & Fiedler 2012). Overall this results reflect the findings on the difference in the species composition of the northern and the southern meadows, that have already been discussed: The guild of grass-feeders was the most affected by the flooding regime and these guild was therefore found more frequently on the northern meadows, whereas the Brassicaceae-feeder *P. rapae* was more common on the southern meadows.

Butterflies inhabiting meadows were relatively more common on the nutrient poor meadows. As already mentioned above the sediments which are more or less regularly delivered to the southern meadows during inundation events act as natural fertilisers, making the southern meadows generally more nutrient rich. But also the northern part of the National Park Donau-Auen contains nutrient rich meadows, whereas some of the southern meadows near the levee are rather nutrient poor. Therefore most of the nutrient poor meadows are found on the northern part of the Nationalpark and reveal relatively more xerothermophilous species. These nutrient poor meadows show less shrub encroachment as almost all of them were completely mown during the 2012 and 2013 survey. Vice versa the contribution of butterfly species inhabiting forest margins was higher on nutrient rich meadows, with a higher proportion of tall perennial herbs.

The hypothesis of a unique species set on annually flood-impacted meadows was already refuted. But some general statements about the distribution of butterfly species relative to their life history traits can be made. On the southern flood-prone meadows one can find relatively more butterflies showing a high fecundity (*Aglais urticae*, *Inachis io, Melitaea aurelia Nymphalis polychloros*) and a long lifespan (*Gonepteryx rhamni, A. urticae, Argynnis paphia, I. io, N. polychloros, Polygonia c-album, Vanessa atalanta, Vanessa cardui)*. There are relatively more migratory (*Colias alfacariensis/hyale*, *Colias crocea*, *P. edusa*, *Vanessa atalanta* and *Vanessa cardui*) and dispersive butterflies (*P. brassicae*, *P. rapae*, *A. urticae*, *I. io*, *N. polychloros*, *P. c-album*) on the southern meadows than on the northern meadows, whereas butterflies with a strong side fidelity are less prevalent on flood-prone meadows (*Heteropterus morpheus*, *Cupido minimus*, *Lycaena dispar, Satyrium w-album, Brenthis daphne, Coenonympha glycerion,).* Even though the southern meadows showed no species composition consisting of true wetland species, the higher average precipitation index of the flood affected meadows indicates that these meadows contain slightly more butterflies living in comparatively wetter habitats.

Assembly rules

As already proven, on the one hand the inundation changes the relative contributions of different guilds (i.e. feeding guild) and functional groups (i.e. dispersion) but on the other hand some functional groups are not directly influenced by the flooding regime (i.e. butterfly groups according to habitat preferences). But all in all, the results show that the composition of functional traits was altered by the flooding regime. Therefore Functional Diversity was expected to be lower on the southern meadows, because some functional traits were supposed to be missing, as the flooding event filters out some traits on the southern meadows. In fact, the Functional Evenness was much more variable but only slightly stronger on the southern than on the northern meadows, indicating the communities of the southern meadows to be rather instable and unsaturated. Functional Divergence was proven to show higher values at higher degrees of limiting similarity ruling community assemblies, in a study using simulated data sets (MOUCHET *et al.* 2010). In this study, Functional Divergence was highest among butterflies at meadows near Orth, which only suffered a medium flooding impact by uprising groundwater, followed by the southern meadows (S). The abundant species of the meadows of these two flooding categories tend to be at the outer margins of the functional space (MASON *et al.* 2005, VILLÉGER *et al.* 2008, MOUCHET *et al.* 2010). Therefore butterfly assemblages on the meadows near Orth (N_O) and the southern meadows (S) are rather ruled by niche differentiation.

Interannual differences in flood intensity

The above considerations are largely related to the survey results in the year 2013, which was characterized by an unusually strong summer flood. Also in 2012, with a much shorter and less intense flooding event, flooding regime was the most crucial factor altering butterfly species composition on the meadows. This proves that the flooding regime is decisive not only in an extreme year, but higher flooding intensity rendered species composition less homogenous. The exceptional flooding of some of the northern meadows in 2013 (N_O and N_S) made their species composition even less homogenous than on the regularly flooded meadows (S). Meadows which were actively flooded (N_S) showed the most heterogeneous species composition. These results corroborate that even if the southern meadows are not inhabited by typical wetland species, their species composition seems to be well adapted to the more or less regular flooding anyway, which was already shown by higher average precipitation indices of the southern meadows.

Although butterfly species composition differed in the homogeneity between the years 2013 and 2012, assemblages were remarkably similar concerning those species which were responsible for the discrimination relative to flooding impact. In total only 13 species contributed 80% of the dissimilarity in species composition and the first nine species were exactly the same in both years. Again the grass-feeders *Maniola jurtina* (16.5%) and *Coenonympha glycerion* (13.1%) were more frequent on the northern part. In contrast to the surveys in 2013, *Pieris rapae* (11.2%) and *Polyommatus icarus* (6.7%) were also more common on the northern meadows in 2012. *Celastrina argiolus* was more frequent in the northern part but contributed only to the top 80% discrimination of the species composition in the year 2013, when this species was more abundant. The highly polyphagous larval stages of *C. argiolus* feed, among others, on woody plants (i.e. *Frangula alnus*) and are therefore probably less affected by flooding events. In contrast to *C. argiolus*, *C. glycerion* seems to suffer from the flooding impact, as it contributed strongly to species composition differentiation only in 2012. All in all, this species was more common in 2012 with approximately twice as much sightings on the northern meadows than on the southern meadows. In 2013 only 30% of the total sightings were done on the southern meadows. *Anthocharis cardamines* and *Zerynthia polyxena* could not alter species composition in 2012, as the surveys were done after their flight periods.

Even though butterfly assemblages on the meadows were made up from pretty similar species in the years 2013 and 2012, multivariate analyses revealed a clear interannual variation. This underlines that abundance fluctuations of ubiquitous species play the crucial role concerning the differences in species composition.

Impact of the mowing regime

Ostensibly, the mowing regime neither influenced butterfly species number nor their overall abundance or species composition in 2013, but slightly affected species composition in 2012. These results are contrary to initial assumptions, as the impacts of mowing on invertebrates are widely discussed to be rather negative (e.g. GERSTMEIER 1996, MORRIS 2000, HUMBERT *et al.* 2009). Indeed, mowing once or twice a year was shown to lead to a decline in butterfly richness and abundance (MORRIS 2000, DOVER *et al.* 2010). Mowing causes direct mortality especially of the immobile stages, leads to a temporary shortage of nectar and changes habitat structures and concomitantly oviposition sites (HUMBERT *et al.* 2009, DOVER *et al.* 2010). These findings could not be affirmed in this study. Notably, mowing took place less regularly in the year 2013 because of the strong inundation and the spatial separation of the meadows. Five of the six mulched meadows of 2013 had still been mown in the year 2012 and none of the meadows in 2012 was categorised as mulched. Therefore mulching was a side effect of the stronger inundation, making the mowing more difficult because of temporally constrained access for the farmers. Against this background, it could have been expected that especially the exceptional mowing regime in 2013 influenced species richness, abundance and species composition. For example the exceptional mulching could have led to a decline in species richness and abundance, as flower nectar availability at the mulched meadows was temporarily almost not-existent. This was not the case, even if flower nectar availability was shown to influence abundance and therefore indirectly species richness. One explanation might be that the effects of mulching on plant species composition, possibly altering host plant species availability to butterflies, would have only been expected if mulching would be done regularly over several years, as described by BAKKER *et al*. (1989) and MOOG *et al.* (2002) after 25 years. Different mowing regimes are therefore no crucial event neither acting on the butterfly species richness and abundance nor on the species composition in a year with strong flooding impact. This underlines the crucial role of the flooding regime. If the flooding event takes place in such an intensive way as in 2013, natural river dynamics surpass the influence of mowing as a management practice. In 2013, even some northern meadows were under water, indicating that in that year flooding indeed surpassed mowing in shaping meadow butterfly assemblages. In order to evaluate the effects of mowing on butterflies at the Nationalpark Donau-Auen, I would suggest repeating the 2013 survey in a year with less flooding impact.

Conservation aspects

With 72 species recorded in the years 2013, 2012 and 2005, butterfly communities in the National Park Donau-Auen are moderately diverse, compared to the 209 species which are known for Austria as a whole (HUEMER 2013) .

On the one hand the representation of species of conservation concern was with 33% much higher than the representation reported for moth species of conservation concern (5%) by TRUXA & FIEDLER (2012). Three butterfly species are listed as strongly endangered on the Red List of Lower Austria, 19 species are listed as endangered and of three species the exact regional status of vulnerability is not known (HÖTTINGER & PENNERSTORFER 1999 cit. in HÖTTINGER *et al.* 2013). Another seven endangered species were only found in the Viennese part of the National Park (HÖTTINGER *et al.* 2013), which could be an indication for their likely occurrence in the Lower Austrian part as well. On the other hand, none of the strongly endangered species was seen more than three times. *Polyommatus semiargus* was seen only twice on a southern meadow and once on a northern meadow. *Zerynthia polyxena* and *Nymphalis polychloros* were both seen only twice on the northern part and *N. polychloros* additionally once on the southern part of the National Park in 2013. On the other hand, *Z.polyxena* and its host plant *Aristolochia clematitis* were seen regularly, implicating this species to be more common in the National Park Donau-Auen than the sampling scheme targeted at meadow butterflies might indicate.

Also the endangered species *Thecla betulae* (1,1), *Satyrium pruni* (0,1), *Satyrium w-album* (3,2), *Apatura ilia* (16,33), *Apatura iris* (1,0), *Limenitis camilla* (3,6) and *Limenitis populi* (2,2), which all inhabit forests and forest margins, were not very frequently seen on the sampling sites. But again sightings besides standardized meadow transects showed at least *S. w-album* and *A. ilia* to be pretty common. It might be reasonably assumed that *T. betulae* and *S. pruni,* whose larvae feed on *Prunus spinosa,* are more common in the Viennese part of the Nationalpark, where *P. spinosa* is part of the shrubs on the so-called “Heißländen”. In fact the National Park is of specific regional importance for all listed species which inhabit forests like *N. polychloros* and especially the floodplain species *L. populi* (2,2) feeding on *Populus nigra* and *Populus tremula* and *A.iris (1,0)* feeding on *Salix sp. A. iris* is not very common in lowlands, as its host plants (i.e. *Salix caprea*) are more frequent in the floodplains of the uplands. In order to get meaningful information about the status of the populations of the species inhabiting woodlands, specially designed surveys should be done, as these species are only found on meadows by chance. Against expectations, the wetland species *Neptis rivularis* (1,0) and *Melitaea diamina* (0,1) were uniques, showing this endangered species to be pretty rare in the National Park as well. Whereas another endangered species, *Lycaena dispar* (13,55), seems to be of least concern in these region, especially on the southern meadows.

Besides the species inhabiting woody or rather wet habitats, the xerothermophilous meadows, which are mostly found in the northern part of the National Park are of importance for several endangered species inhabiting warm and dry sites such as *Polyommatus coridon* (9,1) and *Melitaea didyma* (21,2). Especially the relatively frequent sightings of *Papilio machaon* (15,10) and *Iphiclides podalirius* (3,3) indicate a regional refuge for these endangered species. *Polyommatus dorylas* (0,1) and *Polyommatus thersites* (3,3) as well as *Melitaea aurelia (1,2)* showed no clear preference to the northern meadows. *Polyommatus dorylas* was found on a meadow close to the levee, where this species had been recorded before (FIEDLER pers. comm.).

Numerous sightings of *Plebejus aryrognomon* (48,11) point to a favourable conservation status of this species in the National Park, which is of importance as the conservation status of this species is not known for Lower Austria (HÖTTINGER & PENNERSTORFER 1999 cit. in HÖTTINGER *et al.* 2013). As *Colias alfacariensis* was not distinguished from its sibling species *Colias hyale*, the regional situation of this endangered species could not be assessed. Also the effective proportion of *Cupido decoloratus (7,3*) should be targeted in an additional survey, as this species was only distinguished in 2013. This species is limited to the southern and easternmost part of Austria (STETTMER *et al.* 2011), probably giving the National Park Donau-Auen a special responsibility.

Lower Austria marks the northern distribution boundary of *Melitaea trivia*, but as this species was not found in any of the samplings, its occurrence in the National Park Donau-Auen remains very unlikely. This xerothermophilous species, whose presence is linked to raw soil or rocks, used to be pretty common in eastern Austria, but showed only very local populations. It became endangered through bush encroachment, reforestation and inappropriate habitat management (HÖTTINGER & TIMPE 2003). *M. trivia* is listed as strongly endangered on the Red List of Lower Austria (HÖTTINGER & PENNERSTORFER 1999 cit. in

HÖTTINGER *et al.* 2013). Also the occurrence of *Brenthis hecate* could not be confirmed. *B. hecate* is supposed to be critically endangered in Austria. The only regional host plant of this species is *Filipendula vulgaris*, which is endangered itself but was found on a few meadows in the National Park Donau-Auen. Hence, it is possible that some relict populations of *B. hecate* might still await discovery in the reserve.

Conclusion

The butterfly communities of the meadows of the Nationalpark Donau-Auen are ruled by the flooding. Even if the inundation in 2013 was much more intense as usual, it could generally be shown that the factor flood influences the species abundance and concomitantly the species number as well as species composition strongly. The effects of the mowing only carries weight if the inundation is less intense. The southern meadows are mainly inhabited by the ubiquitous grass-feeders *Maniola jurtina* and *Coenonympha glycerion*, as well as the Pieridae *Pieris rapae*, *Pieris napi* and *Pontia edusa.* It is also likely to find relatively more individuals of *Aglais urticae, Inachis io, Nymphalis polychloros, Vanessa atalanta, Vanessa cardui* and *Polygonia c-album.* Also floodplain species like *Apatura ilia* might be found more frequently on the southern meadows. Xerothermophilous species are more common on the northern meadows, which are generally nutrient poor and harbour dry and warm habitats.

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Appendix

Table 13. Abbreviations of the meadows, their geographic coordinates and various ecological descriptors. Flood regime: N_O – non flooded meadows with high level of groundwater, N_M – non flooded meadows, N_S – non flooded meadows with flood impact only in 2013, S – regularly flooded once a year. Mowing regime: mulched, mown or unmown meadows. Average nectar availability of all sampling periods, scaled from 1 (poor) to 3 (rich). Nutrient level: average of the Ellenberg indicator values for nitrogen of the eponymous species of all plant communities occurring on each meadow.

	GPS Coordinates		Flood regime	mowing regime	nectar availability	area (m	nutrient level
N1	48.141674	16.691097	N_O	mulched	1.3	21040	2
N2	48.139399	16.688560	N_O	mown	0.4	9793	3
N3	48.135885	16.691137	N_O	mown	0.4	3184	2
N4	48.135345	16.726652	N_M	mown	0.5	13097	1
N5	48.137035	16.737446	N_M	mown	0.5	15546	2
N6	48.135388	16.765577	N_M	mown	0.7	20651	3
N7	48.137493	16.770920	N_S	mown	1.3	31297	1
N8	48.142490	16.855506	N_S	mulched	0.2	2105	4
N9	48.144552	16.867415	N_S	unmown	0.8	30521	3
N10	48.142204	16.869153	N_S	mown	0.3	8963	1
N11	48.140085	48.140085	N_M	mown	0.3	41563	3
N12	48.144208	16.686033	N_O	mulched	0.2	12287	1
N13	48.144208	16.686033	N_O	mown	0.4	10922	3
N14	48.138137	16.670047	N_O	mown	0.5	21095	2
N15	48.136634	16.830400	N_M	mown	0.3	5890	1
N16	48.136634	16.830400	N_M	mown	0.8	15237	2
N17	48.136634	16.830400	N_M	mown	0.6	7535	2
N18	48.144208	16.686033	N_M	mown	1	8022	1
N19	48.144208	16.686033	N_M	mown	0.8	7026	1
N20	48.144208	16.686033	N_O	mown	0.6	7311	1
S1	48.131335	16.688436	S	mulched	0.2	8974	1
S2	48.129946	16.679124	S	mown	0.8	53002	1
S3	48.131292	16.674811	S	mown	1.1	39373	1
S4	48.129502	16.712984	S	mown	0.6	25507	2
S5	48.126623	16.717683	S	mown	0.4	12507	2
S6	48.129058	16.720923	S	unmown	0.4	10453	1
S7	48.129058	48.129058	S	mown	0.7	33905	1
S8	48.129058	16.720923	S	mown	0.8	48903	2
S9	48.129058	16.720923	S	mulched	0.5	22458	1
S10	48.129058	16.720923	S	unmown	0.3	8405	1
S11	48.129058	16.720923	S	mulched	0.5	16160	2
S12	48.129058	16.720923	S	mulched	0.3	16057	1
S13	48.127769	16.699594	S	unmown	0.7	4095	1
S14	48.129058	16.720923	S	mown	0.8	29455	2
S15	48.129058	16.720923	S	mown	0.5	31251	1
S16	48.129058	16.720923	S	mown	0.9	8242	1
S17	48.129058	16.720923	S	mown	0.2	31251	1
S18	48.129058	16.720923	S	unmown	0.8	8242	1

Table 14. Species list of butterflies from the surveys in 2013, 2012 and 2005. Species found in the respective year were marked (x). Additionally the species were marked (x) if they were found in the Viennese part of the National Park Donauauen, any time between 1989-2011, data from Höttinger *et al.* (2013). Species only recorded in the Viennese part are written in red.

	2013 survey	2012 survey	2005 survey	(Höttinger *et al.* 2013)
Hesperiidae				
Carcharodus alceae				x
Carterocephalus palaemon			x	x
Erynnis tages	x	x	x	x
Hesperia comma	x	x		x
Heteropterus morpheus	x	x	x	x
Ochlodes sylvanus	x	x	x	x
Pyrgus malvae	x	x	x	x
Spialia sertorius				x
Thymelicus lineola	x	x	x	x
Thymelicus sylvestris	x	x	x	x
Papilionidae				
Iphiclides podalirius	x			x
Papilio machaon	x	x		x
Zerynthia polyxena	x		x	x
Pieridae				
Anthocharis cardamines	x			x
Colias alfacariensis/hyale	x	x		x
Colias crocea	x	x		x
Colias erate	x	x		x
Gonepteryx rhamni	x	x	x	x
Leptidea juvernica/sinapis	x	x		x
Pieris brassicae	x	x		x
Pieris napi	x	x	x	x
Pieris rapae	x	x	x	x
Pontia edusa	x		x	x
Lycaenidae				
Aricia agestis			x	x
Callophrys rubi				x
Celastrina argiolus	x	x	x	x
Cupido alcetas	x			x
Cupido argiades	x	x	x	x
Cupido decoloratus	x			-
Cupido minimus	x	x		x
Glaucopsyche alexis				x
Lycaena dispar	x	x	x	x
Lycaena phlaeas	x	x	x	x
Lycaena tityrus	x	x	x	x
Neozephyrus quercus		x		
Plebejus argus	x	x		x
Plebejus argyrognomon	x	x	x	x
Polyommatus amandus				x
Polyommatus bellargus				x
Polyommatus coridon	x	x		x
Polyommatus dorylas	x			x
Polyommatus icarus	x	x	x	x
Polyommatus semiargus	x	x		
Polyommatus thersites	x		x	x
Satyrium pruni		x	x	x
Satyrium spini				x

Satyrium w-album	x	x		x
Thecla betulae		x		x
Nymphalidae				
Aglais urticae	x		x	x
Apatura ilia	x	x	x	x
Apatura iris	x			x
Aphantopus hyperantus	x	x		x
Araschnia levana	x	x	x	x
Argynnis adippe	x	x	x	x
Argynnis aglaja	x			
Argynnis paphia	x	x		x
Boloria dia	x	x		x
Brenthis daphne	x	x	x	
Brintesia circe	x	x		x
Coenonympha glycerion	x	x	x	x
Coenonympha pamphilus	x	x	x	x
Erebia medusa				x
Inachis io	x	x	x	x
Issoria lathonia	x	x	x	x
Lasiommata maera				x
Lasiommata megera				x
Limenitis camilla	x		x	x
Limenitis populi	x			x
Maniola jurtina	x	x	x	x
Melitaea athalia				x
Melitaea aurelia	x	x		x
Meliaea diamina		x		x
Melitaea didyma	x	x	x	x
Melitea phoebe				x
Melanargia galathea	x	x	x	x
Minois dryas	x	x		x
Neptis rivularis	x			x
Nymphalis antiopa				x
Nymphalis polychloros	x			x
Pararge aegeria	x	x	x	x
Polygonia c-album	x	x	x	x
Vanessa atalanta	x	x	x	x
Vanessa cardui	x	x		x

Table 15. Conservation status according to the Red Lists of the butterflies of Austria 2005 (Höttinger & Pennerstorfer 2005, cit. in Höttinger *et al.* 2013) in (RL-A 2005), of Lower Austria 1999 Höttinger & Pennerstorfer 1999 cit. in Höttinger *et al.* 2013) (RL-LA 1999) and of Vienna 2013 (Höttinger *et al.* 2013) (RL-V 2013). Categories of RL-A 2005 and RL-V 2013: RE=regionally extinct, CR=critically endangered, EN=endangered, VU=vulnerable, DD=Data deficient, NT=near threatened, LC=least concern, categories of RL-LA 1999: 0= extinct, 1=threatened with extinction 2=strongly endangered, 3=endangered, 4=potentially endangered, 5=vulnerability not exactly known, 6= vulnerability not sufficiently known, I=vulnerable migratory species, +=not endangered, -= not listed. *Melitaea cinxia* was not listed in Höttinger *et al.* 2013.

	RL-A 2005	RL-LA 1999	RL-V 2013
Hesperiidae			
Carcharodus alceae	NT	3	LC
Carterocephalus palaemon	LC	+	NT
Erynnis tages	LC	+	LC
Hesperia comma	LC	+	VU
Heteropterus morpheus	NT	+	VU
Ochlodes sylvanus	LC	+	LC
Pyrgus malvae	LC	+	VU
Spialia sertorius	VU	3	CR
Thymelicus lineola	LC	+	LC
Thymelicus sylvestris	LC	+	LC
Papilionidae			
Iphiclides podalirius	NT	3	VU
Papilio machaon	LC	3	VU
Zerynthia polyxena	NT	2	EN
Pieridae			
Anthocharis cardamines	LC	+	LC
Colias alfacariensis/hyale	NT/LC	3/+	VU/LC
Colias crocea	NE	I	NE
Colias erate	LC	+	LC
Gonepteryx rhamni	LC	+	LC
Leptidea reali/sinapis	-/DD	/-6	/-DD
Pieris brassicae	LC	+	LC
Pieris napi	LC	+	LC
Pieris rapae	LC	+	LC
Pontia edusa	LC	+	LC
Lycaenidae			
Aricia agestis	NT	+	NT
Callophrys rubi	LC	+	VU
Celastrina argiolus	LC	+	x
Cupido alcetas	-	-	-
Cupido argiades	LC	+	LC
Cupido decoloratus	LC	5	VU
Cupido minimus	LC	+	NT
Lycaena dispar	LC	3	NT
Lycaena phlaeas	LC	+	LC
Lycaena tityrus	LC	+	LC
Neozephyrus quercus	NT	+	LC
Plebejus argus	NT	+	NT
Plebejus argyrognomon	NT	5	VU
Polyommatus amandus	LC	3	CR
Polyommatus bellargus	NT	3	VU
Polyommatus coridon	NT	3	VU
Polyommatus dorylas	VU	3	RE
Polyommatus icarus	LC	+	LC
Polyommatus semiargus	LC	2	CR
Polyommatus thersites	VU	3	VU

Satyrium pruni	NT	3	EN
Satyrium spini	NT	3	VU
Satyrium w-album	VU	3	EN
Thecla betulae	NT	3	NT
Nymphalidae			
Aglais urticae	LC	+	LC
Apatura ilia	NT	3	NT
Apatura iris	LC	3	VU
Aphantopus hyperantus	LC	+	LC
Araschnia levana	LC	+	LC
Argynnis adippe	NT	+	VU
Argynnis aglaja	LC	+	VU
Argynnis paphia	LC	+	LC
Boloria dia	LC	+	NT
Brenthis daphne	LC	+	DD
Brintesia circe	LC	+	LC
Coenonympha glycerion	LC	+	LC
Coenonympha pamphilus	LC	+	LC
Erebia medusa	NT	+	CR
Inachis io	LC	+	LC
Issoria lathonia	LC	+	LC
Lasiommata maera	LC	2	RE
Lasiommata megera	LC	+	LC
Limenitis camilla	LC	3	EN
Limenitis populi	VU	3	CR
Maniola jurtina	LC	+	LC
Melanargia galathea	LC	+	LC
Melitaea athalia	LC	+	VU
Melitaea aurelia	VU	5	RE
Melitaea cinxia	-	-	-
Melitaea diamina	NT	3	RE
Melitaea didyma	VU	3	DD
Melitaea phoebe	VU	3	EN
Minois dryas	NT	+	NT
Neptis rivularis	NT	3	LC
Nymphalis antiopa	LC	3	EN
Nymphalis polychloros	NT	2	VU
Pararge aegeria	LC	+	LC
Polygonia c-album	LC	+	LC
Vanessa atalanta	LC	+	LC
Vanessa cardui	NE	+	NE

Table 16. Number of individuals of each species, counted per site over all sampling periods, in the 2013 survey.

	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11	N12	N13	N14	N15	N16	N17	N18	N19	N20
Hesperiidae																				
Erynnis tages	0	0	0	0	0	0	2	9	22	2	6	0	0	0	0	7	6	3	1	0
Heteropterus morpheus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperia comma	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0
Ochlodes sylvanus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	4	0	1	0	0
Pyrgus malvae	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Thymelicus lineola	3	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	4
Thymelicus silvestris	3	2	0	0	0	0	1	0	0	0	0	2	2	0	0	0	0	1	0	0
Papilionidae																				
Iphiclides podalirius	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Papilio machaon	0	0	0	1	2	1	3	1	0	0	1	0	0	0	1	3	2	0	0	0
Zerynthia polyxena	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Pieridae																				
Anthocharis cardamines	3	0	0	3	7	1	4	4	9	4	3	4	1	8	0	4	0	1	3	3
Colias alfacariensis/hyale	0	0	0	0	2	0	2	4	0	0	0	0	0	0	0	2	2	0	1	0
Colias crocea	0	0	0	0	1	1	3	2	1	0	1	0	0	0	1	3	2	0	0	0
Colias erate	0	2	0	0	3	0	0	3	0	1	0	0	0	0	0	1	0	0	0	0
Gonepteryx rhamni	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	1	1	1	0	0
Leptidea juvernica/sinapsis	17	6	0	2	4	22	23	10	8	4	10	0	4	1	1	10	2	4	4	3
Pieris brassicae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieris napi	7	0	2	3	4	9	16	3	7	2	4	3	3	7	3	12	4	12	9	1
Pieris rapae	9	4	6	14	44	22	63	7	27	4	26	7	12	12	13	69	10	11	18	5
Pontia eudusa	2	0	1	0	2	0	0	0	0	2	1	0	2	0	0	1	0	3	0	0
Lycaenidae																				
Celastrina argiolus	1	1	3	2	3	0	3	0	0	0	3	0	6	3	2	1	1	0	2	4
Cupido alcetas	0	0	0	0	0	1	3	0	0	0	1	0	2	0	1	0	2	0	0	0
Cupido argiades	9	1	0	3	9	16	43	2	4	0	2	1	4	1	5	22	1	6	14	1
Cupido decoloratus	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0	2	0	1	0	0
Cupido minimus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lycaena dispar	1	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycaena phlaeas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Lycaena tityrus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0

Plebejus argus	0	1	0	0	0	11	6	0	10	0	0	0	0	0	0	0	2	0	0	0
Plebejus argyrognomon	0	2	0	0	0	11	6	0	12	0	1	0	0	0	0	0	0	0	0	0
Polyommatus coridon	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0
Polyommatus dorylas	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyommatus icarus	3	5	2	2	23	17	43	4	13	0	9	4	1	6	2	28	9	5	25	8
Polyommatus semiargus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyommatus thersites	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Satyrium w-album	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphalidae																				
Aglais urticae	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Araschnia levana	0	0	6	2	4	0	6	6	6	7	17	0	1	2	14	0	0	0	3	0
Apatura ilia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Apatura iris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphantopus hyperantus	0	9	0	2	1	1	0	0	0	0	0	1	5	8	0	0	0	0	2	0
Argynnis adippe	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argynnis aglaja	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argynnis paphia	4	1	1	0	1	0	0	0	3	0	0	4	5	6	0	1	1	0	1	1
Brenthis daphne	3	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Brintesia circe	1	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boloria dia	1	1	1	5	32	12	10	2	1	0	0	1	0	0	3	7	1	7	5	4
Coenonympha glycerion	41	98	26	7	56	71	26	9	30	1	13	4	49	6	6	68	14	13	0	0
Coenonympha pamphilus	1	0	0	1	4	3	14	13	5	0	2	0	2	1	1	7	1	2	0	0
Inachis io	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	6	0	0	0	0
Issoria lathonia	1	0	1	0	1	1	1	0	7	0	2	1	1	1	0	4	0	1	1	0
Limenitis camilla	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Limenitis populi	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Maniola jurtina	79	42	12	48	96	32	27	6	20	1	15	24	53	34	13	72	8	28	0	0
Melanargia galathea	3	0	0	0	5	0	2	0	1	0	1	1	4	0	0	0	0	0	1	0
Melitea aurelia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melitaea didyma	0	3	0	3	7	0	5	1	0	0	1	0	0	0	0	0	0	0	0	0
Minois dryas	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Neptis rivularis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Nymphalis polychloros	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Pararge aegeria	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0
Polygonia c-album	0	0	0	1	0	0	0	1	1	0	0	0	1	3	2	2	0	0	2	0

Vanessa atalanta	0	0	0	0	0	3	1	0	3	1	0	0	0	0	0	0	1	1	0	0
Vanessa cardui	0	0	1	1	0	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18
Hesperiidae																		
Erynnis tages	0	1	1	0	0	0	0	6	1	0	1	0	0	0	0	0	0	0
Heteropterus morpheus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperia comma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ochlodes sylvanus	0	0	0	0	0	0	0	3	0	0	0	0	0	2	0	0	0	0
Pyrgus malvae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Thymelicus lineola	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Thymelicus silvestris	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Papilionidae																		
Iphiclides podalirius	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1
Papilio machaon	0	0	1	0	0	0	0	1	0	0	0	0	0	7	1	0	0	0
Zerynthia polyxena	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieridae																		
Anthocharis cardamines	1	2	2	0	0	0	0	0	2	3	0	4	0	3	3	1	0	1
Colias alfacariensis/hyale	0	2	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Colias crocea	0	2	2	0	0	0	2	1	0	0	0	1	0	0	0	0	1	1
Colias erate	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Gonepteryx rhamni	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Leptidea juvernica/sinapsis	6	1	0	2	0	0	2	6	1	2	1	0	1	15	3	3	6	1
Pieris brassicae	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Pieris napi	9	31	6	13	0	6	13	0	12	6	3	1	6	11	24	8	3	5
Pieris rapae	12	35	10	15	2	6	23	33	14	10	10	6	10	64	26	17	18	16
Pontia daplidice	0	1	0	0	0	0	1	3	0	0	1	0	0	0	0	3	0	1
Lycaenidae																		
Celastrina argiolus	2	4	6	3	5	1	12	1	2	0	1	2	12	0	3	1	1	2
Cupido alcetas	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cupido argiades	1	9	6	9	0	1	3	9	0	0	0	0	1	3	1	0	1	0
Cupido decoloratus	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Cupido minimus	0	1	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0
Lycaena dispar	0	0	1	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0
Lycaena phlaeas	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0

Lycaena tityrus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Satyrium w-album	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Plebeius argus	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plebejus argyrognomon	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyommatus coridon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyommatus dorylas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyommatus icarus	0	18	15	14	2	1	1	9	0	0	1	0	1	5	7	4	2	1
Polyommatus semiargus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Polyommatus thersites	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Nymphalidae																		
Aglais urticae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Araschina levana	4	16	35	7	3	9	11	1	1	4	0	0	5	31	12	2	6	1
Apatura ilia	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Apatura iris	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Aphantopus hyperantus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argynnis) adippe	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Argynnis aglaja	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Argynnis paphia	1	6	8	3	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Brenthis daphne	0	0	0	0	0	0	0	0	0	0	0	0	2	5	1	0	0	0
Brintesia circe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Boloria dia	0	0	0	1	0	0	0	1	1	0	0	0	0	1	2	0	1	0
Coenonympha glycerion	0	6	1	0	1	0	0	13	0	0	0	0	0	3	3	2	2	1
Coenonympha pamphilus	0	3	0	0	0	0	0	2	0	0	0	0	0	0	6	3	0	1
Inachis io	1	2	10	1	1	5	4	5	1	0	1	0	8	6	1	1	0	1
Issoria lathonia	0	2	0	0	0	0	1	7	2	0	0	0	2	2	3	1	0	0
Limenitis camilla	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Limenitis populi	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Maniola jurtina	3	16	31	7	4	1	10	17	11	0	3	0	10	42	6	16	9	2
Melanargia galathea	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Melitaea aurelia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melitaea didyma	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Minois dryas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neptis rivularis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphalis polychloros	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pararge aegeria	0	0	0	4	0	0	0	1	1	0	0	3	0	0	0	0	0	0

Polygonia c-album	2	1	7	1	0	0	0	1	0	0	0	0	0	1	1	2	1	3
Vanessa atalanta	2	2	1	1	0	2	0	0	0	0	0	1	1	0	0	1	2	0
Vanessa cardui	0	0	1	0	0	0	0	5	0	0	0	0	0	4	0	1	0	0

Table 17. Number of individuals of each species, counted per site over all sampling periods, in the 2012 survey.

	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11	N12	N13	N14
Hesperiidae														
Erynnis tages	0	1	0	1	0	0	0	2	1	1	2	0	0	0
Heteropterus morpheus	2	1	0	0	0	0	0	0	0	0	0	0	0	0
Hesperia comma	0	0	0	0	1	0	1	0	0	0	0	1	0	3
Ochlodes sylvanus	2	1	1	0	0	0	0	0	0	1	0	1	8	5
Pyrgus malvae	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Thymelicus lineola	9	1	9	1	3	35	13	2	0	7	1	17	5	11
Thymelicus silvestris	0	1	0	0	0	0	0	0	0	0	0	5	0	7
Papilionidae														
Papilio machaon	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pieridae														
Colias alfacariensis/hyale	0	0	0	1	0	1	1	2	0	0	0	0	0	0
Colias crocea	0	0	0	3	0	1	1	1	1	1	2	0	0	0
Colias erate	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Gonepteryx rhamni	1	2	2	0	0	1	3	1	1	0	0	0	0	0
Leptidea juvernica/sinapsis	3	0	3	0	0	5	26	5	1	15	2	17	3	3
Pieris brassicae	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Pieris napi	0	1	5	1	2	1	3	0	1	1	3	3	1	4
Pieris rapae	8	4	1	8	15	12	31	7	15	10	11	5	6	13
Lycaenidae														
Celastrina argiolus	0	0	1	3	7	0	1	0	1	1	0	1	4	5
Cupido argiades	0	2	0	5	2	8	15	2	4	9	1	3	0	11
Cupido minimus	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Lycaena dispar	0	0	4	0	0	0	0	0	0	0	0	2	0	0
Lycaena phlaeas	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Lycaena tityrus	0	0	0	0	7	0	0	0	0	0	0	0	1	0
Neozephyrus quercus	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Plebejus argus	1	1	0	0	0	18	3	17	15	2	0	0	0	0
Plebejus argyrognomon	0	2	0	1	2	3	4	2	2	0	0	0	0	0
Polyommatus coridon	0	0	0	0	0	4	0	0	1	0	0	0	0	0
Polyommatus icarus	1	1	1	10	7	11	25	16	3	2	12	7	1	5
Polyommatus semiargus	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Satyrium pruni	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Satyrium w-album	0	0	0	0	0	0	0	0	2	0	0	0	1	0
Thecla betulae	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Nymphalidae														
Apatura ilia	0	0	0	1	2	0	1	0	3	0	3	1	0	3
Aphantopus hyperantus	2	14	4	7	2	1	1	0	1	0	1	7	14	3
Araschnia levana	0	0	2	0	0	1	0	0	0	1	3	0	1	3
Argynnis adippe	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Argynnis paphia	2	9	1	2	7	1	2	0	0	2	2	4	22	2
Boloria dia	6	11	0	6	64	32	26	6	17	6	17	3	0	2
Brenthis daphne	2	0	9	0	0	0	1	0	0	0	0	2	4	2
Brintesia circe	0	0	1	2	0	0	0	0	1	0	0	0	0	0
Coenonympha glycerion	31	10	17	0	11	31	33	22	20	7	4	13	0	9
Coenonympha pamphilus	1	1	0	1	8	1	12	21	0	2	1	1	2	11
Inachis io	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Issoria lathonia	0	0	0	1	2	0	3	2	0	0	2	0	0	0
Maniola jurtina	51	47	86	56	108	63	107	19	31	26	25	88	39	54
Melanargia galathea	48	6	0	3	49	14	35	32	4	4	2	24	8	9
Melitaea aurelia	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Melitaea diamina	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melitaea didyma	0	1	0	1	2	7	7	1	0	0	1	0	0	1
Minois dryas	0	0	0	0	0	1	3	3	0	0	3	0	0	0
Pararge aegeria	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Polygonia c-album	0	0	0	2	2	0	0	1	3	0	2	1	2	1
Vanessa atalanta	1	0	1	0	0	0	1	1	0	0	0	0	0	1
Vanessa cardui	0	0	0	0	0	0	4	0	0	0	0	0	1	0

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13
Hesperiidae													
Erynnis tages	0	1	0	1	0	0	0	2	1	1	2	0	0
Heteropterus morpheus	2	1	0	0	0	0	0	0	0	0	0	0	0
Hesperia comma	0	0	0	0	1	0	1	0	0	0	0	1	0
Ochlodes sylvanus	2	1	1	0	0	0	0	0	0	1	0	1	8
Pyrgus malvae	0	0	0	0	0	0	0	0	1	0	0	0	0
Thymelicus lineola	9	1	9	1	3	35	13	2	0	7	1	17	5

Thymelicus silvestris	0	1	0	0	0	0	0	0	0	0	0	5	0
Papilionidae													
Papilio machaon	0	0	0	0	0	0	0	0	0	0	0	0	1
Pieridae													
Colias alfacariensis/hyale	0	0	0	1	0	1	1	2	0	0	0	0	0
Colias crocea	0	0	0	3	0	1	1	1	1	1	2	0	0
Colias erate	0	0	0	1	0	0	0	0	0	0	0	0	0
Gonepteryx rhamni	1	2	2	0	0	1	3	1	1	0	0	0	0
Leptidea juvernica/sinapsis	3	0	3	0	0	5	26	5	1	15	2	17	3
Pieris brassicae	0	0	0	0	0	0	1	0	0	0	0	0	1
Pieris napi	0	1	5	1	2	1	3	0	1	1	3	3	1
Pieris rapae	8	4	1	8	15	12	31	7	15	10	11	5	6
Lycaenidae													
Celastrina argiolus	0	0	1	3	7	0	1	0	1	1	0	1	4
Cupido argiades	0	2	0	5	2	8	15	2	4	9	1	3	0
Cupido minimus	0	0	0	1	0	0	0	0	0	0	0	0	0
Lycaena dispar	0	0	4	0	0	0	0	0	0	0	0	2	0
Lycaena phlaeas	0	0	0	0	0	0	1	0	0	1	0	0	0
Lycaena tityrus	0	0	0	0	7	0	0	0	0	0	0	0	1
Neozephyrus quercus	1	0	0	0	0	0	0	0	0	0	0	0	0
Plebejus argus	1	1	0	0	0	18	3	17	15	2	0	0	0
Plebejus argyrognomon	0	2	0	1	2	3	4	2	2	0	0	0	0
Polyommatus coridon	0	0	0	0	0	4	0	0	1	0	0	0	0
Polyommatus icarus	1	1	1	10	7	11	25	16	3	2	12	7	1
Polyommatus semiargus	1	0	0	0	0	0	0	0	0	0	0	0	0
Satyrium pruni	0	0	0	0	0	1	0	0	0	0	0	0	0
Satyrium w-album	0	0	0	0	0	0	0	0	2	0	0	0	1
Thecla betulae	0	0	0	0	1	0	0	0	0	0	0	0	0
Nymphalidae													
Apatura ilia	0	0	0	1	2	0	1	0	3	0	3	1	0
Aphantopus hyperantus	2	14	4	7	2	1	1	0	1	0	1	7	14
Araschnia levana	0	0	2	0	0	1	0	0	0	1	3	0	1
Argynnis adippe	0	0	0	0	0	0	1	0	0	0	0	0	0
Argynnis paphia	2	9	1	2	7	1	2	0	0	2	2	4	22

Boloria dia	6	11	0	6	64	32	26	6	17	6	17	3	0
Brenthis daphne	2	0	9	0	0	0	1	0	0	0	0	2	4
Brintesia circe	0	0	1	2	0	0	0	0	1	0	0	0	0
Coenonympha glycerion	31	10	17	0	11	31	33	22	20	7	4	13	0
Coenonympha pamphilus	1	1	0	1	8	1	12	21	0	2	1	1	2
Inachis io	0	0	0	0	0	0	0	1	0	0	0	0	0
Issoria lathonia	0	0	0	1	2	0	3	2	0	0	2	0	0
Maniola jurtina	51	47	86	56	108	63	107	19	31	26	25	88	39
Melanargia galathea	48	6	0	3	49	14	35	32	4	4	2	24	8
Melitaea aurelia	0	0	1	0	0	0	0	0	0	0	0	0	0
Melitaea diamina	0	0	0	0	0	0	0	0	0	0	0	0	0
Melitaea didyma	0	1	0	1	2	7	7	1	0	0	1	0	0
Minois dryas	0	0	0	0	0	1	3	3	0	0	3	0	0
Pararge aegeria	0	0	0	0	0	0	0	0	0	0	1	0	0
Polygonia c-album	0	0	0	2	2	0	0	1	3	0	2	1	2
Vanessa atalanta	1	0	1	0	0	0	1	1	0	0	0	0	0
Vanessa cardui	0	0	0	0	0	0	4	0	0	0	0	0	1

Table 18. Number of individuals of each species, counted per site over all sampling periods, in the 2005 survey.

	14	15	16	17	18	26	36	37	38	39	40	44
			N2	N1			N12			N13	N14	
Hesperiidae												
Carterocephalus palaemon	0	0	0	0	1	0	0	0	0	0	0	0
Erynnis tages	0	0	0	0	1	0	0	0	0	0	0	0
Heteropterus morpheus	0	0	0	0	0	0	0	0	1	0	0	0
Ochlodes sylvanus	0	0	0	0	0	0	0	0	0	0	0	2
Pyrgus malvae	0	0	0	0	0	0	0	0	0	0	0	0
Thymelicus lineola	0	1	0	0	0	0	0	0	0	0	1	2
Thymelicus sylvestris	0	0	0	0	0	0	0	0	0	0	0	0
Papilionidae												
Zerynthia polyxena	0	0	0	0	0	0	0	0	0	0	0	0
Pieridae												
Antocharis cardamines	0	4	0	0	0	0	0	0	0	0	0	0
Colias hyale	0	1	0	0	0	0	0	0	0	0	0	0
Gonepteryx rhamni	0	0	0	3	0	0	0	0	0	0	0	0
Pieris napi	1	0	2	0	0	0	0	0	0	0	3	1
Pieris rapae	0	0	1	1	1	0	0	2	2	0	1	2
Pontia edusa	0	0	0	0	0	0	0	0	0	0	0	0
Lycaenidae												
Aricia agestis	1	0	0	0	0	0	0	0	0	0	0	0
Celastrina argiolus	0	0	0	0	0	0	0	0	0	0	0	0
Cupido argiades	0	0	0	0	0	0	0	0	0	0	0	0
Lycaena dispar	0	0	0	0	0	0	0	0	0	0	0	0
Lycaena phlaeas	0	0	0	0	0	0	0	0	0	0	0	0
Lycaena tityrus	0	0	0	1	0	0	0	0	0	0	0	0
Plebeius argyrognomon	0	0	0	0	0	0	0	0	0	0	1	3
Polyommatus icarus	18	13	4	3	5	1	3	32	0	1	11	10
Polyommatus thersites	0	0	0	0	0	0	0	0	0	0	0	0
Satyrium pruni	0	0	0	1	0	0	0	0	0	0	0	0
Nymphalidae												
Aglais urticae	0	0	0	0	0	0	0	0	0	0	0	0

Apatura ilia	0	0	2	5	0	0	2	0	0	0	0	0
Araschnia levana	0	0	0	0	0	0	0	0	0	0	0	0
Argynnis adippe	0	0	0	0	0	0	0	0	2	0	0	1
Brenthis daphne	0	0	4	0	1	0	0	2	0	1	0	0
Coenonympha glycerion	30	35	10	7	5	7	1	16	2	22	3	22
Coenonympha pamphilus	7	30	7	3	19	2	6	2	0	0	2	1
Inachis io	0	0	0	0	0	0	0	0	0	0	0	0
Issoria lathonia	0	0	0	0	1	0	0	0	0	0	0	0
Limenitis camilla	0	0	0	1	0	0	0	0	0	1	0	2
Maniola jurtina	77	23	13	6	18	15	6	47	3	27	150	90
Melanargia galathea	2	2	0	0	0	0	0	2	0	7	0	4
Melitaea didyma	9	2	0	0	7	0	0	0	0	0	0	2
Pararge aegeria	0	0	0	0	0	0	0	0	0	0	0	0
Polygonia c-album	0	1	2	0	0	0	2	0	1	2	0	0
Vanessa atalanta	0	0	0	0	0	0	0	0	0	0	0	0
	14	15	16	17	18	26	36	37	38	39	40	44

	1	2	5	8	11	12	13	22	23	29	31	34	45	47	48	50
								S2	S3	S1	S13		S2	S4		S5
Hesperiidae																
Carterocephalus palaemon	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Erynnis tages	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heteropterus morpheus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ochlodes sylvanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyrgus malvae	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Thymelicus lineola	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Thymelicus sylvestris	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Papilionidae																
Zerynthia polyxena	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieridae																
Antocharis cardamines	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Colias hyale	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gonepteryx rhamni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieris napi	36	0	0	1	1	3	0	0	0	1	2	1	1	1	1	1

Pieris rapae	4	3	2	0	1	1	1	1	0	0	0	0	0	1	0	2
Pontia edusa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Lycaenidae																
Aricia agestis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Celastrina argiolus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cupido argiades	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Lycaena dispar	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0
Lycaena phlaeas	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycaena tityrus	1	5	3	0	0	1	1	0	0	0	0	0	0	0	0	0
Plebeius argyrognomon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyommatus icarus	1	1	0	7	1	0	0	13	0	1	2	2	0	1	4	0
Polyommatus thersites	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Satyrium pruni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphalidae																
Aglais urticae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apatura ilia	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	1
Araschnia levana	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Argynnis adippe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brenthis daphne	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Coenonympha glycerion	0	5	0	5	0	1	12	6	1	3	0	14	0	7	2	0
Coenonympha pamphilus	3	36	2	19	4	2	24	2	0	7	0	7	1	0	1	0
Inachis io	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Issoria lathonia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limenitis camilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maniola jurtina	7	52	12	1	28	34	52	158	4	29	6	26	27	37	54	6
Melanargia galathea	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Melitaea didyma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pararge aegeria	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0
Polygonia c-album	0	0	2	1	1	0	0	0	0	1	0	0	4	0	0	0
Vanessa atalanta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 19. Functional traits of the butterfly species of the 2013 survey. Phagism: 0=monophagous, 0.5 = uniphagous, 1=polyphagous species (Bink 1992). Grass: 0=never grass-feeding, 0.5=grass-feeding, 1=exclusively grass-feeding species. Herb: 0=never herb-feeding, 0.5=herb and woody plants feeding, 1=exclusively herb feeding species. Wood: 0=never woody plants feeding, 0.5=woody plants and herb feeding, 1=exclusively woody plants feeding species. Fabaceae: 0=never Fabaceae feeding, 0.5= Fabaceae feeding, 1=exclusively Fabaceae feeding species. Brassicaceae: 0=never Brassicaceae feeding, 0.5=Brassicaceae feeding, 1= Brassicaceae feeding species. Habitat: 1=true meadow species, 1.5=species inhabiting meadows and margins, 2=species inhabiting margins, 2.5= species inhabiting forest margins, 3=species inhabiting forest (Bink 1992, Settele *et al.* 2005). Lifespan: species living 1=10-15 days, 1.5=16-20 days, 2=21-25 days, 2.5=26-35 days, 3=36-45 days, 3.50 >45 days. Length of the forewing: in mm (Slamka 2004). Voltinism: 1= univoltine, 2=polyvoltine species. Fecundity: Species laying 1=40-89 eggs, 1.5=90-134 eggs, 2=135-202 eggs, 2.5=203-303 eggs, 3=304-455 eggs, 3.5=465-1024 eggs (Settele *et al.* 2005). Mean temperature index, mean precipitation index and mean soil water content are taken from (Schweiger *et al.* 2014).

	Phagism	grass	herbs	wood	Fabaceae	Brassicaceae	Habitat	Lifespan	length of the forewing	Voltinism	Fecundity	larval residence	STI (temperature index)	mean precipitation index	mean soil water content
Hesperiidae															
Erynnis tages	0.5	0	1	0	1	0	1	1	13.5	1	1	1	**9.12**	807.99	0.44
Hesperia comma	0.5	1	0	0	0	0	1	2	15	1	1	1	8.47	769.27	0.43
Heteropterus morpheus	0.5	1	0	0	0	0	2	1	17	1	1	1	9.52	764.79	0.42
Ochlodes sylvanus	0.5	1	0	0	0	0	2	1.5	15	1	1.5	1	8.58	777.08	0.44
Pyrgus malvae	0.5	0	1	0	0	0	1	1	12	2	1	1	8.74	765.57	0.43
Thymelicus lineola	0.5	1	0	0	0	0	2	1	14	1	2	1	8.69	736.42	0.42
Thymelicus sylvestris	0.5	1	0	0	0	0	2	1	13.5	1	2	1	9.87	783.58	0.43
Papilionidae															
Iphiclides podalirius	0.5	0	0	1	0	0	1.5	1.5	38.5	2	2	2	10.87	780.33	0.42
Papilio machaon	1	0	1	0	0	0	1	1.5	45	2	1.5	1	9.28	737.43	0.42
Zerynthia polyxena	0	0	1	0	0	0	2.5	2	26.5	1	1	1	10.67	777.33	0.39
Pieridae															
Anthocharis cardamines	0.5	0	1	0	0	1	1.5	1	21	1	1	1	8.3	778.77	0.44
Colias alfacariensis /hyale	0.5	0	1	0	1	0	1	2	25	2	3	1	9.94	811.35	0.43
Colias crocea	0.5	0	1	0	1	0	1	2	25	2	3	1	10.69	798.28	0.43
Colias erate	0.5	0	1	0	1	0	1	1.5	23.5	2	2.5	1	10.03	632.06	0.34
Gonepteryx rhamni	0.5	0	0	1	0	0	2.5	3.5	28.5	1	2.5	2	8.81	772.47	0.43
Leptidea juvernica/reali	0.5	0	1	0	1	0	1	1	20.5	2	1	1	9.11	770.01	0.43
Pieris brassicae	0.5	0	1	0	0	1	1	1.5	30.5	2	2.5	1	9.29	789.63	0.44
Pieris napi	0.5	0	1	0	0	1	1.5	1	22	2	1.5	1	8.21	793.11	0.45

Pieris rapae	0.5	0	1	0	0	1	1	1.5	23	2	1.5	1	9.63	778.96	0.43
Pontia edusa	1	0	1	0	0	0.5	1	1.5	22	2	2	1	10.43	730.71	0.4
Lycaenidae															
Celastrina argiolus	1	0	0.5	0.5	0.5	0	2.5	1	15	2	1.5	2	9.14	763.1	0.43
Cupido alcetas	0.5	0	1	0	1	0	2	1	14.5	2	1.5	1	10.81	844.04	0.43
Cupido argiades	0.5	0	1	0	1	0	1	1.5	13.5	2	2	1	9.42	766.25	0.42
Cupido decoloratus	0	0	1	0	1	0	1	1	12.5	2	1.5	1	9.57	645.13	0.35
Cupido minimus	0	0	1	0	1	0	1.5	1	12.5	2	1.5	1	8.76	817.26	0.45
Lycaena dispar	0	0	1	0	0	0	1	2	17.5	2	3	1	9.34	706.61	0.39
Lycaena phlaeas	0	0	1	0	0	0	1	1.5	13.5	2	2	1	9.29	787.04	0.44
Lycaena tityrus	0	1	0	0	0	0	1	1	15	2	2	1	9.35	778.38	0.43
Satyrium w-album	0	0	0	1	0	0	3	2.5	15	1	1	3	8.87	768.93	0.43
Plebejus argus	1	0	0.5	0.5	0.5	0	1	2	13.5	2	1	1	8.61	778.56	0.43
Plebejus argyrognomon	0.5	0	1	0	1	0	1	1.5	15	2	2.5	1	9.51	766.48	0.41
Polyommatus coridon	0	0	1	0	1	0	1	2.5	17	1	2	1	9.31	801.21	0.44
Polyommatus dorylas	0	0	1	0	1	0	1	2	16	1	1.5	1	9.32	869.36	0.45
Polyommatus icarus	0.5	0	1	0	1	0	1	1.5	16	2	2.5	1	9.07	789.28	0.44
Polyommatus semiargus	0.5	0	1	0	1	0	1	1.5	15.5	2	2.5	1	7.91	755.5	0.44
Polyommatus thersites	0	0	1	0	1	0	1	1.5	14.5	2	2	1	10.59	791.04	0.42
Nymphalidae															
Aglais urticae	0	0	1	0	0	0	1	3	23.5	2	3.5	1	8.12	781.52	0.44
Apatura ilia	0	0	0	1	0	0	2.5	2	36.5	1	2	3	9.03	776.95	0.42
Apatura iris	0	0	0	1	0	0	2.5	2	37.5	1	1.5	3	8.51	774.96	0.43
Aphantopus hyperantus	0.5	1	0	0	0	0	1	1.5	22	1	2.5	1	7.9	770.27	0.44
Araschina levana	0	0	1	0	0	0	2.5	1	18	2	3	1	8.62	739.43	0.42
Argynnis adippe	0	0	1	0	0	0	2.5	2.5	27	1	1.5	1	8.37	772.92	0.43
Argynnis aglaja	0	0	1	0	0	0	2.5	2	27.5	1	2.5	1	7.79	814.41	0.46
Argynnis paphia	0	0	1	0	0	0	2.5	3	35	1	1.5	1	9.02	777.2	0.43
Brenthis daphne	0	0	0	1	0	0	2.5	2	23.5	1	2	1	10.6	822.57	0.42
Brintesia circe	0.5	1	0	0	0	0	1	2.5	35.5	1	3	1	11.07	796.98	0.41
Boloria dia	0	0	1	0	0	0	1.5	1.5	17	2	1.5	1	9.28	784.27	0.43
Coenonympha glycerion	0.5	1	0	0	0	0	1	1	17	2	1	1	8.06	736.54	0.42
Coenonympha pamphilus	0.5	1	0	0	0	0	1	1.5	15	2	1.5	1	8.96	793.06	0.44
Limenitis camilla	0	0	0	1	0	0	3	1.5	27	1	1.5	2	8.85	815.11	0.45

Limenitis populi	0	0	0	1	0	0	3	1.5	39.5	1	2	3	7.48	769.55	0.44
Maniola jurtina	1	1	0	0	0	0	2.5	2.5	24.5	1	3	1	9.85	797.53	0.43
Melitaea aurelia	1	0	1	0	0	0	1	1.5	16.5	1	3.5	1	8.68	833.3	0.45
Melitaea didyma	1	0	1	0	0	0	1	1.5	20	2	2.5	1	10.42	783.05	0.42
Minois dryas	0.5	1	0	0	0	0	1	2	29	1	2	1	9.52	807.1	0.43
Neptis rivularis	0.5	0	0	1	0	0	2.5	2	25	1	1.5	2	8.23	856.9	0.46
Nymphalis polychloros	1	0	0	1	0	0	2.5	3.5	29.5	1	3.5	3	9.68	760.71	0.42
Inachis io	0.5	0	0.5	0.5	0	0	1	3	30	2	3.5	1	8.12	781.52	0.44
Issoria lathonia	0	0	1	0	0	0	1	1.5	20.5	2	3	1	9.33	748.91	0.41
Melanargia galathea	0.5	1	0	0	0	0	1	2	25.5	1	1.5	1	9.71	782.6	0.43
Pararge aegeria	0.5	1	0	0	0	0	2	1.5	20.5	2	1	1	9.71	775.84	0.43
Polygonia c-album	1	0	0.5	0.5	0	0	2.5	3	23.5	2	1.5	2	8.6	759.35	0.43
Vanessa atalanta	0	0	1	0	0	0	2	3	30	2	2.5	1	9.07	785.78	0.44
Vanessa cardui	1	0	1	0	0	0	1	3	29	2	2.5	1	9.04	770.51	0.43

Abstract

The impact of flooding regimes on temperate-zone butterfly communities has thus far received little attention. Along the river Danube in eastern Austria, a levee built in the late 19th century nowadays largely interrupts natural river dynamics. Only a fraction of the floodplain area still experiences annual inundations during summer after snow-melt in the Alps. Butterfly communities on meadows have to face another crucial and unpredictable event, viz. mowing. To study the influence of these two factors on butterfly communities we repeatedly counted butterflies over a vegetation period on 18 flooded and 20 non flooded meadows. Also a dataset from an earlier survey (2012) at the same region was used, to compare the influence of a strong summer inundation (my survey, 2013) to the influences of a softer inundation (2012). We also assessed the availability of nectar sources and the nutrient status of the meadows. The butterfly species list, containing species that were found in 2013, 2012, 2005 and in the Viennese part (listed by HÖTTINGER *et al.* 2013) contains 84 species, of which three species are listed as strongly endangered and 24 as endangered, on the Red list of Lower Austria. Species number per meadow was exclusively influenced by overall butterfly abundance; in turn, overall butterfly abundance, as expected, was lower on meadows affected by annual flooding. But nevertheless, species accumulation curves suggest that the species richness on the flooded, southern meadows was smaller than on the not flooded, northern meadows. Likewise, as expected, species composition differed significantly relative to flooding regime. Butterfly species which were more common on flooded meadows were not typical wetland species, but rather the most abundant ubiquitous species. Grass-feeders were more affected by flood regime than herb-feeders in general. In particular, Brassicaceae-feeding species of the family Pieridae were relatively more prevalent on nutrient-rich flood-prone meadows. The proportion of migratory and dispersive butterflies, but also butterflies showing a high fecundity and a long lifespan, was higher on flood-prone meadows. On flood-impacted meadows more butterflies were found which are characteristic for more humid habitats. Against expectations, disturbance effects of mowing were outweighed by flooding; mowing shaped species composition only if the annual inundation was less intense. Meadows with medium flooding impact by uprising groundwater (N_O) and annually flooded meadows are ruled by niche differentiation, whereas the butterfly assemblages on meadows without flooding impact are rather ruled by the limiting similarity theory.

Zusammenfassung

Der Einfluss von Überflutung auf Tagfaltergemeinschaften wurde bisher kaum untersucht. Im Nationalpark Donau-Auen erfahren die Tagfaltergemeinschaften südlich des Marchfeld-Schutzdamms, welcher im späten 19. Jahrhundert erbaut wurde, regelmäßige Überflutungen. Die Wiesen nördlich des Damms sind von der Dynamik des Hochwassers abgetrennt. Die Überflutung wird jährlich im Sommer in unterschiedlichem Ausmaße durch die Schneeschmelze in den Alpen verursacht. Neben der Überflutung ist die Mahd der zweite unvorhersehbare Faktor mit welchen die Tagfaltergemeinschaften umgehen müssen. In dieser Studie wurde der Einfluss der Überflutung sowie der Mahd auf die Tagfaltergemeinschaften untersucht. Dazu wurden die Tagfalter auf 20 nicht überfluteten und 18 überfluteten Wiesen über eine Vegetationsperiode hinweg regelmäßig erfasst. Um die Auswirkungen unterschiedlich starker Überflutung auf die Tagfaltergemeinschaften abschätzen zu können wurden Daten aus dem Jahr 2012 und 2005, Jahre mit sehr geringem Hochwasser, mit den Daten dieser Arbeit (2013), mit einem sehr starken Hochwasser, verglichen. Zudem wurde auf jeder Wiese die Nektarverfügbarkeit bewertet sowie der Nährstoffgehalt der Wiesen erfasst. Regressionsanalysen ergaben, dass einzig die Abundanz einen Einfluss auf den lokalen Artenreichtum nimmt. Hingegen zeigen Artenakkumulationskurven, dass weniger Arten des regionalen Artenpools auf den südlichen Wiesen vorkommen. Im Gegensatz zum lokalen Artenreichtum ist jedoch die Abundanz signifikant geringer auf den Wiesen mit Hochwasserreinfluss. Auch die Futtergilden wurden vom Hochwasser verändert. Auf den südlichen Wiesen gab es einen höheren Anteil an Kraut-fressenden und innerhalb dieser Gilde an Brassicaceae-fressenden Schmetterlingen. Auf den nördlichen Wiesen waren die Gras-fressenden Tagfalter relativ gesehen häufiger. Es wurde zudem ein signifikant höherer Anteil an Wanderfaltern, dispersiven Tagfaltern und Tagfaltern mit einer sehr langen Lebensspanne und einer hohen Fekundität auf den überfluteten Wiesen angetroffen. Die Artenzusammensetzung der Tagfalter wurde ebenfalls stark vom Hochwasser beeinflusst. Ebenso wie der Einfluss der Flut, beeinflusste auch der Nährstoffgehalt die Artenzusammensetzung. Entgegen der Erwartungen konnte keine charakteristische Tagfaltergemeinschaft bestehend aus Arten, welche auf feuchte Habitate spezialisiert sind, für die regelmäßig überfluteten Wiesen gefunden werden. In beiden Jahren machten die drei insgesamt häufigsten Arten fast die Hälfte des Unterschiedes zwischen der Artenzusammensetzung im nördlichen und südlichen Teil aus. Dennoch konnten auf den südlichen Wiesen mehr Arten nachgewiesen werden, welche in relativ feuchten Lebensräumen vorkommen. Entgegen aller Erwartungen stellte sich heraus, dass der Faktor Mahd von dem Faktor Flut überlagert wird und nur geringfügigen Einfluss auf die Artenzusammensetzung im Jahr 2012 nahm. Die Tagfaltergemeinschaften der Wiesen mit einem mittleren Einfluss durch den Faktor Flut (N_O) werden von der Niche Differentiation theory bestimmt, die nördlichen Wiesen ohne Einfluss durch die Flut eher durch die Limiting Similarity theory.

Curriculum Vitae

Personal Information

Name:	Rebecca Fies
Nationality:	Germany
Date of birth:	06.03.1988
Location of birth:	Mannheim

Education

since 10/2011	**University of Vienna** / Vienna / Master’s programme Naturschutz und Biodiversitätsmanagement Master’ thesis: “Impact of flood control on the communities of meadow butterflies in the Nationalpark Donau-Auen.“
since 03/2012	**University of Vienna** / Vienna / Master’s programme Botany
2007- 2011	**University of Konstanz** / Konstanz / Bachelor’s Programme Biological Science Bachelor Thesis: “Futterqualität im Wirt-Parasit-System *Daphnia magna- Pasteuria ramosa: Einfluss auf die nächste Generation.*“
2005-2007	Max-Slevogt-Gymnasium / Landau i.d. Pfalz / Abitur
1998-2005	Marienschule (Gymnasium) / Krefeld
1994- 1998	Sollbrüggenschule (Primary School) / Krefeld

Extracurricular activities

04/2007- 07/2007	**Wellington** / New Zealand Voluntary service at Global Volunteer Network
02/2011-05/2011	**Konstanz** / Wollmatinger Ried Placement at Naturschutzbund (NABU)
02/2012	**Thailand** Study tour with the Division of Systematic and Evolutionary Botany through Thailand
04-06/04/2014	**University of Southampton** / Southampton Oral presentation at the Butterfly conservation 7 International Symposium

Professional experience

02-04/2009	**University of Konstanz** / Konstanz Research assistant, Zoology
07-09/2010	**University of Konstanz** / Konstanz Research assistant, Limnology
07-09/2011	**Botanical garden of the University of Konstanz** / Konstanz Research assistant, Botany

Language skills

English, excellent written and spoken
French, good written and spoken

Computer literacy

Microsoft Office, R, ArcGIS, SPADE