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Unpredictable Flood Pulses Govern Beetle Assemblages in the Litter Layer of Hardwood Floodplain Forests

Unvorhersehbare Flutereignisse bestimmen die Käfer-Lebensgemeinschaften in der Laubstreu von Hartholzauen

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Summary: The beetle fauna of the forest floor of hardwood floodplain forests adjacent to Lake Maggiore (Switzerland) was studied. These floodplain forests are influenced by unpredictable flood pulses. A total of 8,676 specimens belonging to 190 species were sampled. It is hypothesized that unpredictable flood pulses, especially during spring (May, June), are severe disturbances of the terrestrial fauna that hamper both α-diversity and density. The following results were obtained:

1. Contrary to the hypothesis, α-diversity and density were high and comparable to values known from oak stands in primeval forests of Central Europe.
2. The floodplain forests were successfully settled mainly by paludicolous and ripicolous rove beetles (Staphylinidae) that have evolved a wide array of avoidance strategies. Eurytopic and silvicolous species were rare.
3. Resilience after flooding was high and had a strong spatial component. Diverse vegetation structures facilitate vertical dispersion of specimens.
4. Turnover rate of species (β-diversity) following spring/summer floods was low.
5. At the fringe of the hardwood forest turnover rate of species (β-diversity) following a winter flood was high. The high value was mainly caused by additional species in spring which already had left the hardwood forest in autumn.

Hence, the results show that unpredictable flood pulses – also during the growing season – are part of natural ecosystem dynamics in floodplain forests. Increased precipitation, as proposed in future by a scenario, will hardly change beetle assemblages already established.

Key words: floods, forest floor, disturbance, diversity, resilience

Zusammenfassung: Die Käferfauna der Bodenstreu wurde in Hartholzauen am Lago Maggiore (Schweiz) untersucht. Diese Hartholzauen sind unvorhersehbaren Flutereignissen ausgesetzt. Insgesamt wurden 8.676 Individuen ausgewertet, die sich auf 190 Arten verteilten. Die Ausgangshypothese war, dass unvorhersehbare Flutereignisse, besonders im Frühjahr (Mai, Juni), für die Bodenfauna deutliche Störungen bedeuten, die sowohl die Artenvielfalt (α-Diversität) als auch die Besiedlungsdichte erniedrigen. Folgende Ergebnisse wurden erzielt:

1. Im Gegensatz zur Ausgangshypothese waren Artenvielfalt (α-Diversität) und Besiedlungsdichte auffallend hoch und vergleichbar mit Werten, wie sie aus Eichenstandorten in Urwäldern Mitteleuropas bekannt sind.
2. Die Hartholzauen wurden besonders erfolgreich durch paludicole und ripicole Kurzflügler (Staphylinidae) besiedelt, die ein weites Spektrum an Vermeidungsstategien evoluiert haben. Eurytope oder silvicole Arten waren selten.
3. Die Elastizität nach Überflutungsereignissen war hoch und hatte eine ausgeprägte räumliche Komponente. Vegetationsstrukturen ermöglichten Vertikaldispersionen der Individuen.
4. Die Arten-Austauschrate (β-Diversität) nach Sommerüberflutungen war gering.

5. Am Rande der Hartholzaue war die Arten-Austauschrate (β-Diversität) nach einer Winterüberflutung hoch. Der hohe Wert wurde wesentlich durch Immigration zusätzlicher Arten im Frühjahr bedingt, die im Herbst zuvor die Hartholzaue verlassen hatten.

Aus den Ergebnissen folgt, dass unvorhersehbare Flutereignisse – auch während der Vegetationsperiode –zur natürlichen Dynamik von Auwäldern gehören. Erhöhte Niederschläge, wie sie für die Zukunft prognostiziert werden, dürften für die etablierten Käfer-Lebensgemeinschaften keine deutlichen Veränderungen bewirken.

Schlüsselwörter: Überflutung, Waldboden, Störung, Diversität, Elastizität

1. Introduction

Riverine floodplains are diverse ecosystems including a rich mosaic of habitat types. According to the habitat-heterogeneity hypothesis (MacArthur 1965), riverine floodplains provide environments for high species numbers (Ward et al. 1999). For example, ground beetles (Carabidae) distributed on exposed riverine sediments respond to sediment size and prefer stony, sandy or silty substrates (Andersen 1978, Meisner 1984, Bates et al. 2007). Whereas α-diversity in less exposed sites at higher elevation clearly depends on the structural heterogeneity of the vegetation (Brose 2003). Sources of habitat recognition for ground beetles are responses to mechanical stimulation (Andersen 1985) or chemical compounds (Evans 1988).

River floodplains are subjected to floods. Such floods are natural phenomena caused by peaks in precipitation and snow smelt in the catchment area. In the temperate region, floods predominate during winter and early spring. However, due to channelization and drainage of wetlands combined with global warming, flooding has increased in frequency, also during the growing season (van Eck et al. 2004). The unpredictable pattern of extreme flood events is obvious (Ilg et al. 2008).

Riverine floodplains are pulsed ecosystems with distinct flow pulses (Junk et al. 1989, Tockner et al. 2000). As exemplified for ground beetles, both flood duration and ground water depth are seen as the two main factors influencing species assemblages (Gerisch et al. 2006). Because they do not tolerate long periods of inundation, ground beetles have evolved avoidance strategies (Siepe 1994) and emigrate with ascending water levels and immigrate again when water levels recede (Adis & Junk 2002). The beetle fauna of floodplains, however, not only includes ground beetles but also numerous further beetle species. Some of these species are of terrestrial origin (i.e. Staphylinidae), while others (i.e. Dytiscidae, Hydrophilidae) are of aquatic origin and, unlike the terricolous ground beetles, are hampered by drought. Droughts also have marked effects on the diversity and distribution of riverine species (Lack 2003).

The aim of the present study was to examine α-diversity and density of beetle assemblages living in a hardwood floodplain forest that is influenced by unpredictable flood pulses during winter months as well as the growing season. Unpredictable flood pulses, especially during the growing season, should act as severe disturbance regimes. I tested the following hypotheses: Unpredictable flood pulses 1: decline α-diversity and 2: impede density of beetle assemblages inhabiting the forest floor of a hardwood floodplain forest.

2. Materials and methods

2.1. Study site description

The one study area is a hardwood floodplain forest of about 100 ha in size that is situated at the northern end of Lake Maggiore (Switzerland) (Fig. 1). It is part of the nature reserve "Bolle di Magadino" and stretches

Fig 1: View of Lake Maggiore and – surrounded by mountain ridges – the Magadino Plain with the Ticino River. The mouth of the canalized Ticino is seen to the left of the birch; the hardwood forest studied (ca. 100 ha.) "Bolle di Magadino" is seen as a dark patch to the right of the birch.
Abb. 1: Blick zum Lago Maggiore und – umgeben von Gebirgsketten – zur Magadino-Ebene mit dem Fluss Ticino. Die Mündung des kanalisierten Ticino liegt rechts von der Birke; die untersuchte Hartholzaue (ca. 100 ha) „Bolle di Magadino" ist als dunkler Fleck links von der Birke erkennbar.

Fig. 2: The lower part of the hardwood floodplain forest usually is flooded twice a year.
Abb. 2: Der tiefer gelegene Teil der Hartholzaue wird durchschnittlich zweimal im Jahr überflutet.

Fig 3: The central part of the hardwood floodplain forest includes dead oak trees (*Quercus robur*). The oldest living oak trees have a diameter of 85 cm (b.h.d.) and are calculated to be > 100 years old. Oak trees probably die because of water stress.
Abb. 3: Die Hartholzaue enthält abgestorbene Eichen (*Quercus robur*). Die ältesten lebenden Eichen haben einen Durchmesser von 85 cm (BHD) und wurden >100 Jahre geschätzt. Eichen sterben möglicherweise durch Wasserstress.

Fig. 4: Several oxbows run through the hardwood forest. An ecotone characterized by rush (*Juncus* spp.) falls dry when the water level drops below 194.00 m.a.s.l.; this enables terrestrial beetles to successfully immigrate to the fringe of the hardwood forest.
Abb. 4: Mehrere Altwässer durchziehen die Hartholzaue. Ein Saumbiotop, charakterisiert durch Binsen (*Juncus* spp.), fällt bei einem Seespiegel < 194.00 m.ü.M. trocken, so dass dann terrestrische Käfer erfolgreich in diese Randzone der Hartholzaue einwandern können.

along the estuary of the Verzasca River (46° 11' N, 8° 51' E). The area is influenced by a subtropical climate. In the floodplain, oak trees (*Quercus robur*) dominate and lime trees (*Tilia cordata*) are scattered (Figs. 2, 3). Some tree specimens are calculated to be > 100 years old; oak trees have a stem diameter at breast height up to 85 cm.

The relief exhibits an intermittent pattern including sand dunes - and gravel deposits at higher elevation (194.75 m.a.s.l.) as well as oxbows (Fig. 4) and ponds where silt sediments are accumulated.

The hardwood forest is partly limited by a lightwood with *Salix cinerea* as the dominant species or by a belt of *Phragmites australis* to the lake and to the river side (south and west). *Juncus* spp. (*J. effusus* was most common among six species present, Nicola Patocchi in lit.) often form dense vegetation stands at the fringe of oxbows. At low water levels (193.00 m.a.s.l.) a mud zone bare of any vegetation limits the floodplain forest.

The hardwood floodplain forest is isolated and does not show any connection to a terrestrial upland forest. A connection to the upland is interrupted by a highway, an industrial zone and agricultural fields situated to north and east.

The other study area is a hardwood floodplain forest at the Maggia delta. It is situated westward of the nature reserve "Bolle di Magadino". This floodplain is not isolated from the terrestrial upland.

2.2. Flooding

The water supply of Lake Maggiore is governed mostly by the inflow of the Ticino, Maggia and Verzasca rivers. These rivers are situated at the northern end of the lake. The outflow of the lake at its southern end of

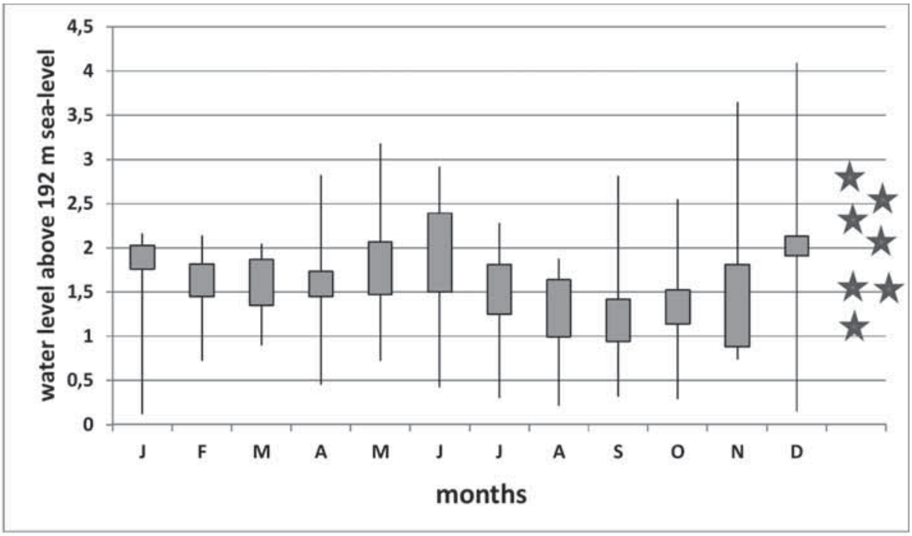

Fig. 5: Water level of Lake Maggiore during the course of the year. The boxes include the upper and the lower median values (above 192 m.a.s.l.) of the monthly maximum – and minimum – water levels during the last ten years (2001-2010). The whiskers include the maximum – and minimum - water levels per month between 2001 and 2010. The asterisks indicate the elevation at which the samplings were taken.
Abb. 5: Wasserspiegel des Lago Maggiore im Jahresgang. Die markierten Flächen schließen die oberen und unteren Mittelwerte (Mediane über 192 m.ü.M.) aus den monatlichen Maximum – und Minimumwerten der letzten zehn Jahre ein (2001-2010). Die Whisker schließen den höchsten und niedrigsten monatlichen Wasserstand in den Jahren 2001 bis 2010 ein. Die Sterne kennzeichnen die Höhenlage, in der die Sammlungen durchgeführt wurden.

distribution follows the Ticino River. Inflow and outflow are rarely equivalent. The lake runs high after snow melt in the Alps or after periods of long-lasting and heavy rain in the catchment area. The boxes in figure 5 enclose the range between the median values of the monthly maximum – and minimum – water levels (data from http://hydrodaten.admin.ch) per month that both varied for the last ten years in about 1m between months. Highest water levels can be expected in May and June and also in December and January (Fig. 5). Lowest water levels occurred from August to September and also in November. The forecast of a water level per months decreases with increasing length of boxes. Extreme deviations from the expected median water levels per month could occur. During the last 10 years, the water level of Lake Maggiore oscillated in a range of 4.10 m. The whiskers in figure 5 include the extreme maximum – and minimum – water levels per month as measured during the last ten years. Pronounced changes in water levels are expected to increase in the climate anticipated in the future, because precipitation events are projected to occur less frequently in summer but more often in spring and autumn (Stoffel & Beniston 2006).

The time interval of submergence at a certain elevation is a further variable determining the occurrence and distribution of beetles. For example, study sites situated at the lower part of the floodplain forest (= 194.00 m.a.s.l.) were not submerged in 2005, whereas in 2008 submergence lasted for 144 days (Fig. 6). The number of flood pulses per year and the period of submergence are independent variables. Two flood pulses exceeded 194.00 m.a.s.l. in 2004 and 2008, as well, and resulted in a submergence interval of the forest floor for 70 and 144 days respectively (Fig. 6). The dark columns in figure 6 indicate the submergence intervals (d) at an elevation >194.25 m.a.s.l.and the light columns submergence intervals (d) at an elevation >194.00 m.a.s.l.. At >194.25 m.a.s.l., the central part of the hardwood forest is submerged. Figure 7 elucidates the submergence intervals at >194.25 m.a.s.l. during May and June from 1998 until 2010.

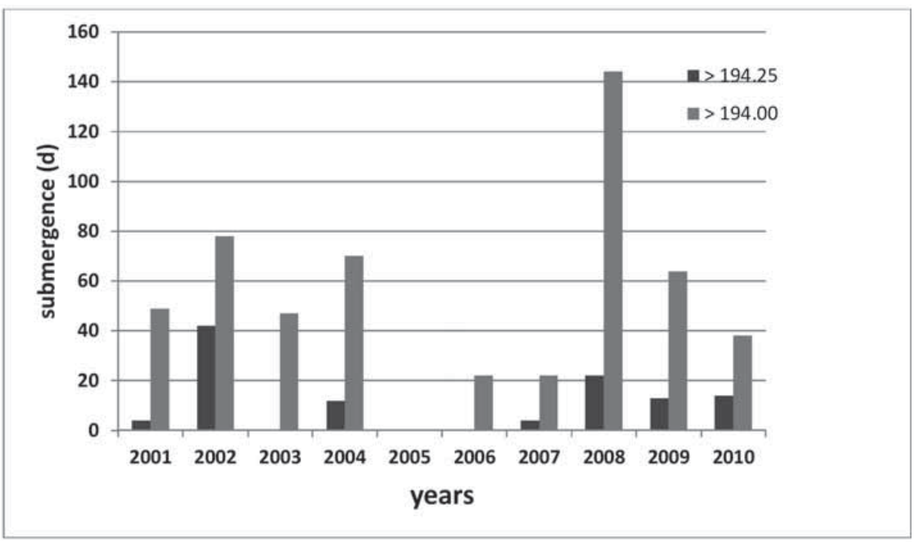

Fig. 6: Days of submergence in the hardwood floodplain forest at elevations above 194.00 and above 194.25 m.a.s.l. from 2001 until 2010.
Abb. 6: Überflutungsdauer (Tage) in der Hartholzaue oberhalb der Höhenlinien von 194.00 und 194.25 m.ü.M. in den Jahren 2001 bis 2010.

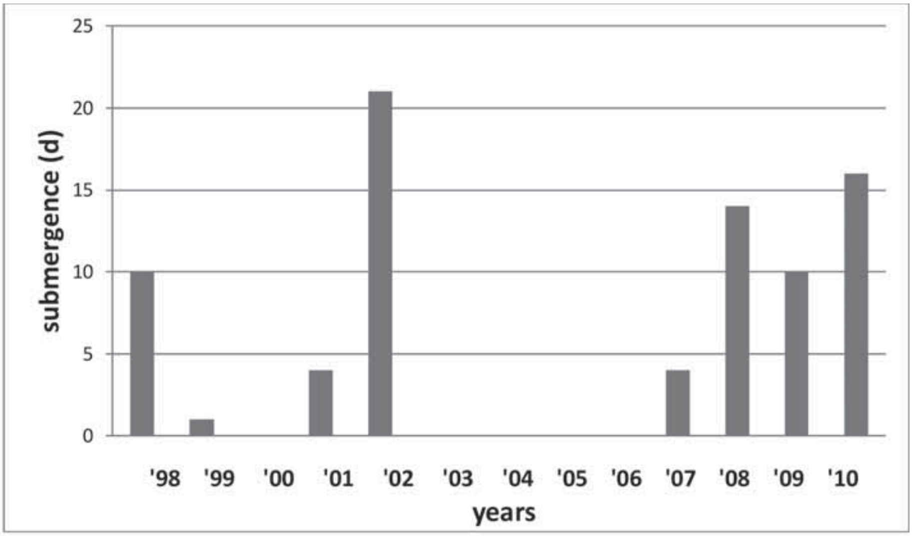

Fig. 7: Days of submergence in the hardwood floodplain forest at an elevation of above 194.25 m.a.s. l. during May and June from 1998 until 2010.
Abb. 7: Überflutungsdauer (Tage) in der Hartholzaue oberhalb der Höhenlinie 194,25 m.ü.M. innerhalb der Monate Mai und Juni von 1998 bis 2010.

2.3. Field sampling and experimental design

The investigation in the nature reserve "Bolle di Magadino" was carried out in 2010 and 2011. In the hardwood floodplain forest the litter layer of the L- and O horizons of the forest floor were sampled at the lower elevated part (series 5 in table 1), the central part (series 6) and at the higher elevated part (series 7) in 1 m² plots, sieved and extracted for soil arthropods using Tullgren funnels. Each series comprised eight replicates. For comparison, additional plots were taken (series 1-4) adjacent to the hardwood forest. These included a lightwood zone, the *Phragmites/Juncus* zone and a mud zone below the vegetation zones.
Samples were chosen randomly above the water line but below the elevation as indicated in the third column of table 1. Only the two series at highest elevation were sampled at dates when the water line was markedly lower than the sampling plots. The mean number of flood pulses and the mean days of submergence per year, as calculated for the last ten years, are shown in table 1 for the elevations including the lightwood and hardwood zone. The asterisks at the right end of figure 5 visualize the elevation at which samples were taken.
The study was completed by hand sampling of beetles in the Maggia delta. Hand-sorted beetles were collected in autumn 2011.
The systematic and nomenclature of the beetles followed Freude et al. (1964-2004), Coiffait (1972-1984) and Köhler & Klausnitzer (1998). Ecological preference groups were assigned according to Koch (1989-1992).

2.4. Data analysis

Data presented in tables and figures were obtained in the nature reserve "Bolle di Magadino". Most of the data were not normally distributed. Therefore, data for α-diversity and density are represented as median and range. I used the non-parametric Mann-Whitney U-test for pair-wise comparison

Tab. 1: Sampling procedure and characterization of sampling plots (1 m²) by number of flood pulses and days of inundation per year as calculated from the last 10 years. Collection for series 1-5 took place above the water line. Each series comprised eight parallels of 1 m².
Tab. 1: Charakterisierung der Sammelflächen (1 m²) hinsichtlich ihrer Lage im Lebensraum und nach den durchschnittlichen Flutereignissen. Berechnet wurden die Anzahl der Überflutungen und die Überflutungsdauer pro Jahr für die letzten zehn Jahre. Die Sammlungen der Serien 1-5 erfolgten oberhalb der Flutlinie. Jede Serie besteht aus acht Parallelen von 1 m².

Series	sampling date	actual water-line (m.a.s.l.)	sampling below (m.a.s.l.)	number (n) of flood pulses	days (n) of sub-mergence	zone
1	25.05.11	192.78	193.00	(not calculated)		mud
2	09.05.11	193.28	193.50	(not calculated)		*Juncus / Phragmites*
3	01.10.10	193.18	193.50	(not calculated)		*Juncus / Phragmites*
4.	01.11.10	193.80	194.00	5.2	53	lightwood
5	29.12.10	193.97	194.25	2.0	11	hardwood
6	11.02.10	(193.59)	194.50	0.9	6	hardwood
7	10.02.10	(193.61)	194.75	0.5	5	hardwood

of data sets. The α-diversity was used to assess the influence of elevation on species richness.

I used β-diversity to determine the species turnover rate between pre- and post flood events and the effect of succession when the water level decreases. β-diversity was calculated using one minus the SØRENSEN index ©. C = 2j/ (a + b), where j is the number of taxa found in both assemblages, a is the number of taxa found in assemblage a, and b is the number of taxa found in assemblage b. β-diversity measures ranges from 0 (indicating identical taxa composition) to 1 (indicating that no taxa are common between assemblages). The two sites (6 vs. 5 in table 1) were not sampled at the same elevation. However, to minimize the effect of elevation, taxa present in a single assemblage but sensitive to moisture were excluded. These were *Tanysphyrus lemnae* and *Arpedium quadrum* at the lower elevation (194.25 m) and *Chalcoides fulvicornis* and *Lordithon thoracicus* at the higher elevation (194.50 m) (Tab. 1, Appendix). Turnover rate measures resilience. There are different meanings of resilience in ecology (GUNDERSON 2000). Here, resilience is the speed by which the system returns to the status quo before a disturbance.

3. Results

3.1. α-Diversity

Beetles settled in all parts of the floodplain. In total, beetle assemblages comprised 8.676 individuals belonging to 190 species. In the hardwood forest, the most common species (> 5 % of a beetles' assemblage) were predatory rove beetles (Tab. 2). At lower elevations several water scavenger beetles (Hydrophilidae) prevailed. Species richness and density of ground beetles was low (Tab. 1, Appendix). However, some species, as exemplified by *Pterostichus oenotrius*, invaded the study plots in higher numbers as soon as the muddy areas fell dry. In the muddy area at lowest elevation (193.00 m.a.s.l.), many

Tab. 2: Common species in a hardwood floodplain forest of the nature reserve "Bolle di Magadino" as well as the number of species and individuals per series. A triangle, ▲, indicates species that accounted for > 5 % of the individuals in an assemblage of eight parallels; + = < 5 %, - = absent.
Tab. 2: Häufige Arten in der Hartholzaue des Naturschutzgebiets „Bolle di Magadino" sowie Arten- und Individuenzahlen für jede Serie. Ein Dreieck, ▲, kennzeichnet Arten, die mit > 5 % der Individuen einer Lebensgemeinschaft (acht Parallelen) vorkamen; + = < 5 %, - = fehlend.

Series	1	2	3	4	5	6	7
Zone	M	J/P	J/P	L	H	H	H
Dytiscidae							
Hydroporus palustris	▲	-	-	-	-	-	-
Hydrophilidae							
Enochrus obscurus	+	+	▲	▲	+	+	-
Anacaena limbata	▲	▲	▲	▲	+	+	-
Cercyon convexiuscula	▲	▲	▲	▲	▲	+	+
Cercyon sternalis	▲	▲	▲	+	+	+	-
Carabidae							
Pterostichus oenotrius	+	▲	+	-	-	-	-
Staphylinidae							
Carpelimus corticinus	▲	+	-	-	+	+	
Carpelimus impressus	+	▲	-	-	-	-	+
Euaestethus ruficapillus	+	+	▲	+	▲	▲	-
Erichsonius cinerascens	+	▲	▲	▲	▲	▲	+
Philonthus micans	+	+	+	+		▲	▲
Schistoglossa viduata	-	-	-	+	+	▲	+
Bibloplectus ambiguus	-	-	+	+	▲	▲	▲
Bryaxis bulbifer	-	+	+	+	▲	▲	▲
Species (n)	50	56	50	49	78	88	76
Individuals (n)	606	817	661	370	1650	3379	1193

predatory diving beetles (*Hydroporus palustris*, Dytiscidae) were present (Tab. 2) although the water level had dropped below sites for a time interval of five days.

Species richness (α-diversity) was highest in the hardwood forest with up to 43 spp./m² (median value: 32 spp./m²). At the lower elevation, adjacent to the hardwood forest, fewer species per m² were found (Fig. 8).

The hardwood floodplain forest situated at the Maggia delta enclosed most of the paludicolous and ripicolous species present in the nature reserve "Bolle di Magadino". However, in this floodplain forest additional flightless ground beetles were present. *Carabus granulatus*, *Pterostichus niger* and *Abax continuus* give examples.

3.2. Density

The density of beetles depended on the elevation of the forest floor. Density was highest in the central part of the hardwood forest with 779 exx./m² (median value: 368 exx./m²) (Fig. 9). At the fringe of the hardwood forest situated adjacent to the

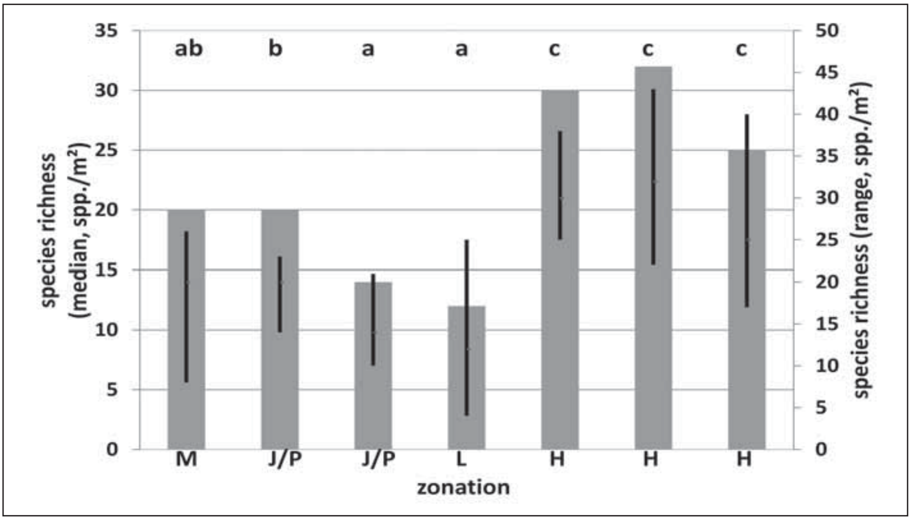

Fig. 8: Number of species (α-diversity, median and range) in the hardwood forest (H) compared to sites at lower elevation (M = mud, J/P = *Juncus/Phragmites*, L = lightwood zone (n = 8). Different letters indicate significant differences.

Abb. 8: Artenvielfalt (α-Diversität, Median und Spannweite) in der Hartholzaue (H) im Vergleich zu den Flächen in geringerer Höhenlage (M = Schlickfläche, J/P = *Juncus/Phragmites*-Fläche, L = Weichholzaue, n = 8). Verschiedene Buchstaben zeigen signifikante Unterschiede an.

lightwood zone (series 5, Tab. 1) and also at higher elevation distant from water bodies (series 7, Tab.1), density was lower. Lowest values were calculated for the vegetation zones and the muddy zone that stretch at lower elevation along the hardwood forest (Fig. 9).

In the hardwood forest, the proportion of aquatic beetles was 14 % or less (Fig. 10). At highest elevation (series 7) only a few specimen of *Cercyon convexiuscula* were found. The vegetation zones situated below the hardwood forest harbored a proportion of about 50 % aquatic beetles. In these series (series 1-4) 12 to 16 species contributed to the aquatic fauna. In total, 41 aquatic species were found, including the collections outside of the study plots (Tab. 1, Appendix).

3.3. Habitat preference

Most species that were found in the hardwood forest are known to prefer swamps and wet habitats and belong to a group of species classified as being paludicolous. Paludicolous and ripicolous species made up about 85 % or more of beetle assemblages. The only exception was the uppermost elevation (194. 75 m.a.s.l.) At this elevation, 75 % paludicolous specimen accounted for the beetle assemblage (Tab. 3).

In parallel with increasing elevation, the number of species and individuals that are not specific to certain habitats (eurytopic) or that prefer forest habitats (= silvicolous) increased (Tab. 3). The species numbers of eurytopic species living at higher elevation (i.e. 194.50 and 194.75 m.a.s.l.) was even higher than that of the paludicolous species. At highest elevations (table 3), the richness of the silvicolous species almost equaled the richness of the paludicolous species. However, individuals of these ecological groups were relatively rare and attained in maximum for the uppermost elevations of only 17 % and 7 % respectively (Tab. 3).

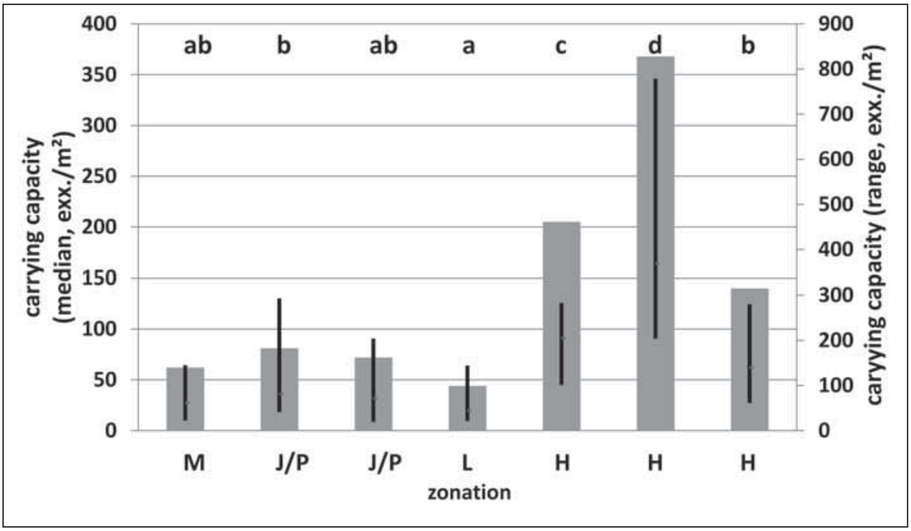

Fig. 9: Density (median and range) in the hardwood forest (H) compared to sites at lower elevation (M = mud, J/P = *Juncus/Phragmites*, L = lightwood zone (n = 8). Different letters indicate significant differences.

Abb. 9: Besiedlungsdichte (Median und Spannweite) in der Hartholzaue (H) im Vergleich zu den Flächen in geringerer Höhenlage (M = Schlickfläche, J/P = *Juncus/Phragmites*-Fläche, L = Weichholzaue, n = 8) Verschiedene Buchstaben zeigen signifikante Unterschiede an.

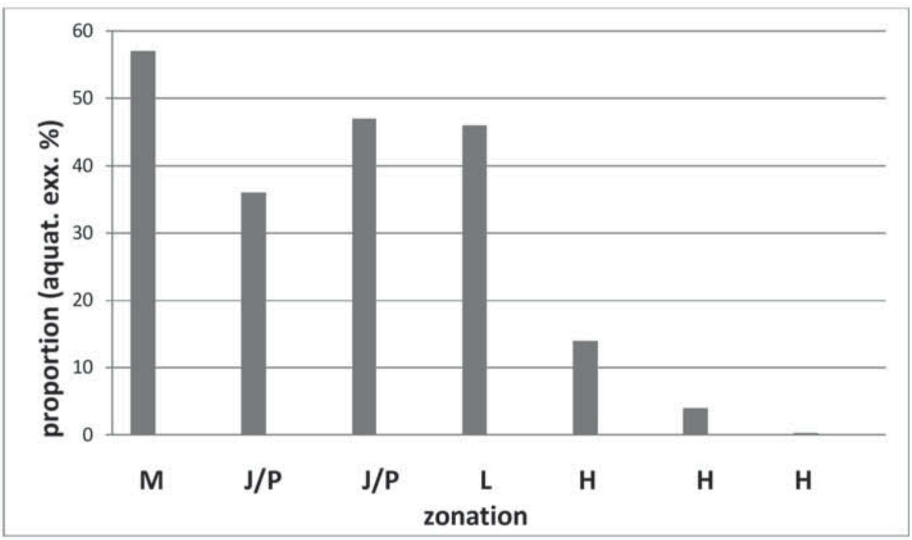

Fig. 10: Proportion of aquatic individuals in respect to total beetle assemblages in the hardwood forest (H) compared to sites at lower elevation (M = mud, J/P = *Juncus/Phragmites*, L = lightwood zonation (sum of n = 8)).

Fig. 10: Anteil aquatisch lebender Käfer an den Käfer-Lebensgemeinschaften in der Hartholzaue (H) im Vergleich zu den Flächen in geringerer Höhenlage (M = Schlickfläche, J/P = *Juncus/Phragmites*-Fläche, L = Weichholzaue (Summe von n = 8)).

Tab. 3: Classification of terrestrial beetles according to ecological preference groups for species (n) and individuals (%) at different elevations. The series and vegetation zones are indicated (see tab. 1). Assemblages are classified according to beetles that either preferred wet habitats, such as swamps (paludicolous), or are mainly found directly on the water's edge (ripicolous), that were mainly restricted to forests (= silvicolous), or exhibited no preference to certain habitats (= eurytopic). Beetles of further preference groups were omitted.

Tab. 3: Klassifikation der terrestrisch lebenden Käfer in ökologische Präferenzgruppen für Arten (n) und Individuen (%) in verschiedenen Höhenlagen. Sammelserien und Vegetationszonen sind angegeben (vgl. Tab. 1). Die Lebensgemeinschaften wurden nach Käfern unterschieden, die entweder feuchte Habitate wie Sumpfflächen und Uferlinien bevorzugen (paludicol, ripicol), die überwiegend in Wäldern leben (silvicol), oder die keine Präferenz zeigen (eurytop). Arten weiterer Präferenzgruppen wurden nicht berücksichtigt.

series	1	2	3	4	5	6	7
zone	M	J/P	J/P	L	H	H	H
paludicolous/ripicolous							
spp. (n)	46	49	23	22	34	31	23
exx. (%)	98	97	86	87	84	85	75
eurytopic							
spp. (n)	2	3	11	7	20	35	31
exx. (%)	-	1	10	11	10	9	17
silvicolous							
spp. (n)	3	2	-	1	5	12	18
exx.(%)	1	-	-	-	1	2	7

3.4. Immigration

As soon as the water level declines, terrestrial species either followed the receding floods from the hardwood forest to the lower elevation or immigrated from areas outside of the hardwood forest. Species following the receding floods were those that presumably hibernated in high numbers within the hardwood forest (Tab. 1, Appendix). These were several rove beetles such as *Erichsonius cinerascens, Philonthus micans, Oxytelus rugosus, Myllaena intermedia* and *Gnypeta carbonaria*. Others occurred in low numbers at higher elevation or were not found in the hardwood forest at all. These species presumably immigrated to the muddy areas in spring (Tab. 1, Appendix). Immigrants included many ground beetles, such as *Pterostichus oenotrius* (Tab. 2), *Agonum duftschmidti, Oodes helopioides* and *Bradycellus collaris*, rove beetles of the genus *Carpelimus* (*C. opacus, C. rivularis and C. impressus*) and *Heterocerus fenestratus* (Heteroceridae). These species are known to prefer open habitats along rivers and can be classified as ripicolous.

3.5. Resilience

Beetles collected at the elevation of 193.50 m.a.s.l. were collected before and after a winter flood (series 3 vs. 2, table 1) that lasted for 6 months at this elevation. Sampling occurred when the floods had receded from the sampling area for a time interval of 14 days. The turnover rate (β-diversity) between beetle assemblages was calculated as 0.48, i.e. about every 2nd species found within the plots after the flood did not occur in these sites before the flood. α-diversity after flooding has increased (Fig. 8).

Beetles collected at 194.50 m were sampled before inundation (February 2010), whereas beetles collected at194.25 m were sampled after inundation (December 2010). Between these sampling dates two floods occurred,

Tab. 4: Species turnover (β-diversity) after influence of a winter flood, after two summer floods, and between adjacent habitats when water level recedes. The second column indicates the time interval the plots have fallen dry after flooding when sampled.

Tab. 4: Arten-Austauschrate (β-Diversität) nach Einfluss einer Winterüberflutung, von zwei Sommerüberflutungen und zwischen benachbarten Flächen bei zurückweichender Flutlinie. In der zweiten Spalte ist die Zeitspanne angegeben, in der die Sammelflächen nach einer Überflutung trocken gefallen waren.

	time interval of flooding	sampling plots above water line after flooding	effect	turnover rate
series 3 vs. 2	6 months	14 days	winter flood	0.48
series 6 vs. 5	14 days, and 3 days	6 months	floods in May and June	0.33
series 2 vs. 1	7 months	5 days	receding floods	0.37

one in May and the other in June, submerging the sampling plots for a time interval of 14 days and 3 days respectively (table 4). (By comparing both sampling dates, the effect of elevation was minimized; see material and methods). The fauna sampled during pre- and post flood months changed less than after the winter flood. A turnover rate of 0.33 ± 0.09 was obtained. (Without correction, a turnover rate of 0.35 ± 0.11 was calculated.) α-diversity did not alter (Fig. 8). Species assemblages of the series 2 vs. 1 were compared for calculating the effect of the receding flood. The sample sites at the lower elevation have falling dry for a time interval of five days subsequent to a submergence period of about 7 months (table 4). The calculated turnover rate was 0.37.

4. Discussion

In the hardwood floodplain forest α-diversity and carrying capacity of the litter layer were remarkable high and resemble values known from the litter layer of undisturbed primeval oak forests in the lower mountain range (Topp et al. 2006). However, differences between beetle assemblages of both ecosystems are evident. In the oak forest of the lower mountain range, many species belonging to different feeding groups such as fungivores, herbivores and carnivores dominated (Topp et al. 2006). In contrast, carnivorous beetles that are adapted to moist habitats were by far the most common feeding group in the hardwood floodplain forest.

In river-floodplain ecosystems, flood pulses seem to be the most important physical variable altering the distribution and abundance of organisms in tropical (Junk et al. 1989) and temperate riverine ecosystems (Tockner et al. 2000) as well. The best documented example concerning beetles can be found in the study by Ilg et al. (2008) on ground beetles. Ground beetles that inhabit the riverine grasslands of Central Europe in high numbers decreased significantly in α-diversity and abundance after a severe summer flood. The lowered values of both variables were still evident during the year following the flood. Two years after the flood, an immigration of mainly eurytopic species of the open landscape resulted again in pre-flood values of α-diversity and abundance (Ilg et al. 2008). Ground beetles, although they have evolved a wide array of adaption mechanisms to withstand or to avoid winter floods, are seen as unable to cope with summer floods because of their specific developmental cycles (Ilg et al. 2008, further citations in Adis & Junk 2002).

Changes between beetle assemblages in the floodplain forest following a flood in spring (May and June) were considerably less pronounced than calculated for ground beetle assemblages at pre- and post flood events (Ilg et al. 2008). The turnover rate (β-diversity) for beetle assemblages in a floodplain forest after spring floods was low and corresponded to ß-diversity values calculated in the flooded grassland ecosystem either between subsequent pre-flood years or between subsequent post-flood years (Ilg et al. 2008).

Similar to ground beetles (Adis & Junk 2002) rove beetles have evolved a complex survival pattern to avoid or to resist winter flooding. However, the survival pattern of paludicolous and ripicolous rove beetles exceeds that of eurytopic ground beetles in respect to unpredictable flooding during summer months. Many rove beetles are predisposed to living in unstable habitats by a large set of avoidance strategies. Several species are covered by a wax layer that prevents moistening and thus enables them to crawl on the water film to reach grasses or drifting material and take off thereafter, others are capable to taking off directly from the water surface. Consequently, not only horizontal emigration on the forest floor, as observed in most ground beetles, but additionally vertical emigration is a successful strategy.

Even when rove beetles are able to avoid unpredictable summer floods by flight, they are unable to withstand flooding in most of their flightless immature stages. Mortality of larvae may result in decreasing population densities. However, sharp decreases in population density can be minimized by risk strategies of females, including both the start of oviposition within the year and the length of oviposition. Onset of reproduction in the field can occur in all months of the year. It varies between species and also between females of a certain species. Most females do not put all eggs into one basket but are able to stretch the period of oviposition over several months. Moreover, seasonal plasticity is evolved because females of the same species behave differently and are either dominated by r-selection or exhibit attributes of K-selection (Topp 1994).

The ability of rove beetles to withstand flooding may even exceed that of ground beetles because of their tiny shape. A small rove beetle may find an air bubble in the soil and may survive flooding in this way. A small and elongate body also helps to survive submergence because oxygen can diffuse from water through a stretched abdomen to the interior even though breathing organs are not evolved. Such diffusion occurs in rove beetles living at the marine coast (Topp & Ring 1988).

General ecological concepts of disturbances and resilience have been developed (Peterson et al. 1998). Resilience of beetles living in floodplains has a strong spatial component as shown by Bengtsson (2002) for soil animals. In floodplain grasslands (Ilg et al. 2008) that are dominated by eurytopic ground beetles, long-distance dispersal of individuals, particularly by horizontal emigration to adjacent upland areas, increases the chance of later (re)immigration (Adis & Junk 2002). However, resilience is low (Fig. 11 a).

In floodplain forests dominated by paludicolous and ripicolous rove beetles, short distance dispersal of individuals, particularly by vertical emigration to adjacent structures above the flooded area, increases the chance of later (re)immigration. Resilience is high (Fig. 11 b).

In the uppermost part of the hardwood floodplain forest density of beetles was significantly lower than in the other parts. The flooding events may provide an expla-

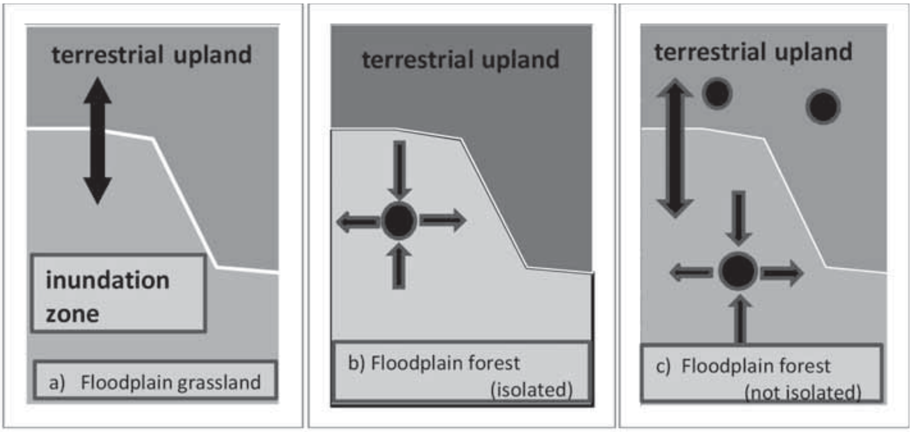

Fig. 11: Examples of faunal responses to flooding: **a** In riverine grasslands resilience is low. The beetle assemblage is influenced by long-distance dispersal of mainly eurytopic species (Ilg et al. 2008). **b** In an isolated floodplain forest resilience is high. The beetle assemblage is influenced by short-distance dispersal of mainly paludicolous species (this study). **c** In a floodplain forest (not isolated) resilience is a mixture of a and b. However, the proportion of eurytopic species with long distance dispersal was low.

Abb. 11: Beispiel für die Reaktionsmuster von Arten in Auenlandschaften vor und nach einer Überflutung: **a** In einem ufernahen Weideland ist die Elastizität gering. Die Käfer-Lebensgemeinschaft wird durch die Ausbreitung überwiegend eurytoper Arten über große Distanz bestimmt (Ilg et al. 2008). **b** In einem isoliert gelegenen Auwald ist die Elastizität hoch. Die Käfer-Lebensgemeinschaft wird durch die Ausbreitung überwiegend paludicoler Arten über kurze Distanz bestimmt (diese Untersuchung). **c** In einem nicht isoliert gelegenen Auwald erfolgt die Elastizität als Mischung von a und b. Allerdings war der Anteil eurytoper Arten mit Ausbreitung über große Distanz gering.

nation. The paludicolous beetles may be less adapted to areas were flooding only occurs every second year, on average. Another explanation may be the isolation of the hardwood floodplain forest from upland forests. In the nature reserve "Bolle di Magadino" isolation prevents a successful immigration of flood-susceptible species from upland forests. Flightless ground beetles of the genera *Carabus, Pterostichus* and *Abax* give examples. Some of which occurred in considerable numbers in the hardwood floodplain forest of the Maggia-delta .

When a floodplain forest is not isolated, but rather stretches to the terrestrial upland, a combination of long-distance and short-distance dispersers can be expected (Fig. 11c). Thus, a further increase in α-diversity and carrying capacity than found in the nature reserve "Bolle di Magadino" at highest elevation can be supposed. A floodplain ecosystem exhibiting no barrier to the upland and mirroring the situation in figure 11c has also been identified in a softwood forest in the floodplain of the River Rhine. This floodplain forest is dominated by eurytopic and silvicolous ground beetles (Topp et al. 2008).

The turnover rate (ß-diversity) of beetle assemblages calculating the effect of a winter flood resulted in a higher value than calculating the turnover rate following floods in May and June. This implies, firstly, that the hardwood floodplain forest harbors relatively stable beetle assemblages and, secondly, that many additional species are able to immigrate in spring. Species that were collected outside of the sampling plots confirmed this implication (Table 1, Appendix). Flood pulses – even during summer – are seen as natural disturbances on previously established beetle assemblages living in the litter layer. Disturbances are followed by a relatively fast (re)immigration of species and reorganization of species assemblages. This is in contrast to many assemblages of soil animals, which are also impacted by pulse disturbances such as clearcutting and drought (BENGTSSON 2002).

Calculating the number of heavy precipitations in a greenhouse-climate-scenario, the water level will further increase during spring and autumn but decrease during summer (STOFFEL & BENISTON 2006). The beetle assemblages of the hardwood floodplain forest dominated by paludicolous and ripicolous species will hardly suffer from these climatic changes.

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Appendix: Distribution pattern of species in the floodplain forest of the nature reserve “Bolle di Magadino”. The numbers refer to the number of individuals in eighth parallels, 1 m² each, of a series. Series were taken at different elevation (m.a.s.l.) and different vegetation zones (M = mud zone, J/P = *Juncus/Phragmites* zones, L = lightwood zone, H = hardwood zones). Species collected outside of the sampling plots are listed in the column “add”.
Anhang: Verteilungsmuster der Arten im Auwald des Naturschutzgebietes „Bolle di Magadino“. Die Zahlen geben die Anzahl der Individuen in acht Parallelflächen von jeweils 1 m² einer Serie an. Die Serien wurden für unterschiedliche Höhenlagen (m.ü.M.) und verschiedene Vegetationszonen ausgewählt. Nachweise von Arten außerhalb der Referenzflächen sind in der Spalte „add“ angegeben.

series	1	2	3	4	5	6	7	add
elevation (m.a.s.l.)	193,0	193,5	193,5	194,0	194,25	194,5	194,75	
vegetation zone	M	J/P	J/P	L	H	H	H	
Carabidae								
Dyschirius globosus		3	2	1	8	15	1	
Dyschirius agnatus								x
Dyschirius intermedius								x
Elaphropus parvulus								x
Stenolophus mixtus	1							
Bembidion lampros					1			
Bembidion azurescens								x
Bembidion quadrimaculatum								x
Bembidion articulatum								x
Acupalpus parvulus								x
Acupalpus dubius					1	9	2	
Pterostichus strenuus						1		
Pterostichus oenotrius	18	54	9					
Pterostichus nigrita		2						
Agonum duftschmidti	18	17		3	3			
Platynus obscurus		1				2		
Amara curta								x
Oodes helopioides	6	5						
Badister sodalis							1	
Badister collaris	5	15	1	1	1	5	4	
Badister peltatus		5						
Demetrias monostigma					1			
Haliplidae								
Haliplus heydeni								x
Noteridae								
Noterus clavicornis	1		1					
Dytiscidae								
Hydroglyphus pusillus								x
Bidessus unistriatus								x
Hygrotus inaequalis			1					
Coelambus impressopunctatus								x
Hydroporus palustris	48		5		4			
Hydroporus angustatus	1				1			
Graptodytes pictus								x
Laccophilus ponticus	17	4						
Laccophilus minutus								x
Copelatus haemorrhoidalis	4	1		1				

Appendix: Continued.
Anhang: Fortsetzung.

series	1	2	3	4	5	6	7	add
elevation (m.a.s.l.)	193,0	193,5	193,5	194,0	194,25	194,5	194,75	
vegetation zone	M	J/P	J/P	L	H	H	H	
Platambus maculatus								x
Rhantus latitans				1				
Rhantus bistriatus	1							
Hydaticus seminiger								x
Hydraenidae								
Hydraena palustris			1	1				
Hydraena testacea			1	10				
Limnebius atomus	10	6	10	4	1		1	
Hydrochidae								
Hydrochus carinatus	10	11	44	1	5			
Spercheidae								
Spercheus emarginatus	1	1						
Hydrophilidae								
Helophorus brevipalpis	25	9			1			
Coelostoma orbiculare				1				
Cercyon convexiuscula	43	59	44	15	94	40	2	
Cercyon sternalis	35	96	6	3	43	41		
Hydrobius fuscipes				2				
Anacaena limbata	124	92	153	99	74	4		
Laccobius striatulus								x
Laccobius minutus								x
Helochares obscurus	14	12	44	26	8	1		
Enochrus coarctatus	4	3	5	3	1			
Enochrus affinis					1			
Enochrus testaceus		2	1	1		1		
Enochrus ochropterus		1						
Berosus signaticollis								x
Silphidae								
Phosphuga atrata								x
Ptiliidae								
Ptinella limbata				1	1	1		
Pteryx suturalis						47	1	
Smicrus filiformis			1					
Acrotrichis brevipennis						1		
Acrotrichis cf. *matthewsi*						1		
Staphylinidae								
Neuraphes elongatulus						4	10	
Stenichnus collaris						2	3	
Euconnus denticornis							1	
Euconnus wetterhali		1			5	12	11	
Scaphisoma agaricinum						1		
Proteinus brachypterus						1	9	
Proteinus macropterus						1		
Micropeplus marietti							1	
Arpedium quadrum				37	10			

Appendix: Continued.
Anhang: Fortsetzung.

series	1	2	3	4	5	6	7	add
elevation (m.a.s.l.)	193,0	193,5	193,5	194,0	194,25	194,5	194,75	
vegetation zone	M	J/P	J/P	L	H	H	H	
Anthobium atrocephalum					2	6		
Carpelimus opacus		35	2		2	4		
Carpelimus bilineatus		5	1	1				
Carpelimus rivularis	..10	..20	3		1			
Carpelimus nitidus		1					2	
Carpelimus impressus	28	218	3		1		1	
Carpelimus corticinus	32	1			2	8	10	
Carpelimus punctatellus							1	
Carpelimus gracilis	2							
Anotylus rugosus	18		1	10	10	13		
Anotylus nitidulus	1							
Bledius femoralis	1							
Stenus comma								x
Stenus juno				3	5			
Stenus clavicornis	1		1		3	1		
Stenus boops				2		2	4	
Stenus argus					2	62	9	
Stenus nanus				4				
Stenus fornicatus	2				2			
Stenus pallitarsus								x
Stenus gallicus		1			1			
Euaestethus ruficapillus		5	95	5	96	249		
Paederus melanopus					5	19		
Astenus immaculatus					3	12	10	
Medon ripicola			1	1				
Scopaeus laevigatus	3	6	7	1	9	18	8	
Lathrobium terminatum	4	10	13	5	44	105	22	
Lathrobium castaneipenne				1			1	
Lathrobium volgense								x
Lathrobium brunnipes				2	2	2		
Lathrobium fovulum	7	5	5	13	14	1		
Lathrobium longulum			6		31	28	41	
Lathrobium magistrettiorum					1	1		
Gauropterus fulgidus								x
Gyrohypnus liebei						1		
Gyrophypnus angustatus			1					
Erichsonius cinerascens	10	32	65	82	229	104	9	
Philonthus nigrita					1			
Philonthus fumarius				1	2			
Philonthus umbratilis			1					
Philonthus mannerheimi							1	
Philonthus quisquiliarius	5	2						
Philonthus micans	8	33	7	3	49	178	96	
Gabrius pennatus	3	1	17	6	21	19	2	
Gabrius sexualis			3					

Appendix: Continued.
Anhang: Fortsetzung.

series	1	2	3	4	5	6	7	add
elevation (m.a.s.l.)	193,0	193,5	193,5	194,0	194,25	194,5	194,75	
vegetation zone	M	J/P	J/P	L	H	H	H	
Ocypus cf. *winkleri*						1		
Ocypus nero								x
Quedius limbatus								x
Habrocerus capillaricornis					3	1		
Ischnosoma splendidus			1		15	22	6	
Lordithon thoracicus						11	3	
Sepedophilus marshami							3	
Sepedophilus stoeckli					3			
Sepedophilus pedicularius							2	
Tachyporus abdominalis							1	
Tachyporus formosus						1		
Tachyporus solutus							4	
Tachyporus hypnorum								x
Tachyporus pusillus							1	
Deinopsis erosa		1	1					
Myllaena intermedia	12	12	32	2	91	137	18	
Cypha discoidea					1	1		
Gyrophaena bihamata						3	1	
Gyrophaena lucidula					4	19	17	
Schistoglossa viduata				3	14	207	28	
Schistoglossa gemina				6	30	90	44	
Tachyusa objecta		1						
Tachyusa coarctata								x
Gnypeta carbonaria	20		2		22	4		
Dacrila fallax					1	1		
Aloconota subgrandis		1						
Liogluta microptera		1						
Atheta elongatula		5						
Atheta hygrobia	13	7	18		4			
Atheta terminalis					8	34	18	
Atheta ganglbaueri						1		
Atheta palustris	2	1						
Atheta viennensis						1		
Atheta sodalis							1	
Atheta hybrida	2							
Atheta basicornis		1			5			
Atheta crassicornis							1	
Acrotona parens							1	
Drusilla canaliculata							3	
Parocyusa rubicunda			4					
Amarochara forticornis			1		2	9	3	
Bibloplectus ambiguus			26	1	278	943	375	
Bibloplectus pusillus				1	18			
Batrisodes delaporti							1	
Batrisodes buqueti						1		

Appendix: Continued.
Anhang: Fortsetzung.

series	1	2	3	4	5	6	7	add
elevation (m.a.s.l.)	193,0	193,5	193,5	194,0	194,25	194,5	194,75	
vegetation zone	M	J/P	J/P	L	H	H	H	
Bryaxis bulbifer		2	3	5	236	580	225	
Rybaxis longicornis					15	27	15	
Brachygluta fossulata					3	2	1	
Brachygluta spec.						2	1	
Brachygluta perforata					2	13		
Bythinus reichenbachi								x
Pselaphaulax dresdensis		1						
Cantharidae								
Cratosilis laeta								x
Elateridae								
Agrilus obscurus								x
Synoptus filiformis								x
Scirtidae								
Cyphon padi	2	2	7			2	10	
Cyphon coarctatus	1							
Buprestidae								
Trachys minutus							1	
Dryopidae								
Dryops luridus		1		1				
Heteroceridae								
Heterocerus fenestratus	5	10						
Dermestidae								
Trinodes hirtus		1						
Byrrhidae								
Pelochares versicolor		1	1				1	
Aspidiphoridae								
Aspidiphorus orbiculatus							1	
Nitidulidae								
Stelidota geminata			2	3	2	3		
Epuraea unicolor								x
Epuraea ocularis								x
Monotomidae								
Monotoma brevicollis	17							
Silvanidae								
Silvanus unidentatus	1							
Phalacridae								
Stilbus oblongus								x
Cryptophagidae								
Cryptophagus corticinus							1	
Cryptophagus scanicus					1	2		
Atomaria mesomelaena						1		
Atomaria fuscata					1	1		
Atomaria fuscicollis				1	1			
Atomaria lewisi					1			
Ephistemus globulus					1	1		

Appendix: Continued.
Anhang: Fortsetzung.

series	1	2	3	4	5	6	7	add
elevation (m.a.s.l.)	193,0	193,5	193,5	194,0	194,25	194,5	194,75	
vegetation zone	M	J/P	J/P	L	H	H	H	
Rhizophagidae								
Rhizophagus bipustulatus						1	1	
Rhizophagus ferrugineus						2		
Lathridiidae								
Enicmus transversus					1			
Lathridius constrictus						1		
Corticarina similata					7	14	48	
Corticarina gibbosa					1	8	9	
Corticarina fuscula.						1		
Colydiidae								
Coxelus pictus						3		
Corylophidae								
Sericoderus lateralis					4	11	3	
Orthoperus intersitus							1	
Clypastraea pulchella							3	
Silvanidae								
Airophilus elongatus								x
Psammoecus bipunctatus								x
Endomychidae								
Endomychus coccineus								x
Coccinellidae								
Stethorus punctillum					1	1	8	
Scymnus auritus				1		1	1	
Coccidula scutellata	1							
Coccidula rufa								x
Halyzia sedecimpunctata							1	
Harmonia axyridis				1				
Propylaea quadripunctata				1		1		
Anisosticta novemdecimpunctata								x
Hippodamia tredecimpunctata								x
Scarabaeidae								
Aphodius prodromus								x
Cerambycidae								
Pogonocherus hispidus							1	
Chrysomelidae								
Chalcoides fulvicornis						20	10	
Plagiodera versicolora								x
Aphthona nonstriata					1			x
Apthona lutescens				1	7	9	10	x
Longitarsus holsaticus								x
Scolytidae								
Xyleborus saxeseni	2	1						
Xyleborus spec.	1	2						
Curculionidae								
Acalles parvulus						4	18	

Appendix: Continued.
Anhang: Fortsetzung.

series	1	2	3	4	5	6	7	add
elevation (m.a.s.l.)	193,0	193,5	193,5	194,0	194,25	194,5	194,75	
vegetation zone	M	J/P	J/P	L	H	H	H	
Acalles lemur							9	
Acalles roboris							2	
Dryopherus corticalis							2	
Dorytomus filirostris						4		
Dorytomus affinis							2	
Tanysphyrus lemnae	5	11	3	2	35			
Limnobaris t-album				1				
Trachodes hispidus							1	
Protapion fulvipes					2	6	18	
Bagous collignensis						1		
Nanophyes marmoratus							1	
Poophagus sisymbri								x
Mononychus punctum-album								x

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