

Effects of floodplain-meadow conservation management on invertebrates, a literature review

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1. Introduction

Aim and content

The aim of this literature review is to describe the conservation interest of invertebrate fauna of traditionally managed floodplain meadows in order to facilitate conservation management that caters for both plants and animals. The study summarizes published literature to identify which invertebrate species and groups are distinctive for floodplain meadows or play an important part in the functioning of the floodplain meadow ecosystem (chapter 3). It then identifies the ecological impact (ecosystem services) of these species groups (chapter 4) and identifies their main habitats and host species within floodplain meadows (chapter 5). Chapter 6 describes how floodplain meadow invertebrates cope with flooding events and chapter 7 summarizes the existing knowledge base for impacts of conservation management, particularly mowing and grazing, on invertebrates in floodplain meadows. Finally, all main findings and recommendations are summarized in chapter 8.

Definitions and focus

For this literature study, floodplain meadows are defined in line with Peterken (2013) as unimproved grasslands that are seasonally inundated with freshwater. This definition excludes reed beds and salt marshes as well as improved grasslands (MG6 and MG7 of the National Vegetation Classification (Rodwell 1992)). In the UK floodplain meadows encompass mostly *Sanguisorba officinalis* - *Alopecurus pratensis* (great burnet-meadow foxtail) grassland (MG4), but may include other grasslands too, particularly MG5, *Cynosurus cristatus* - *Centaurea nigra* (crested dog's tail-common knapweed) in higher, less frequently inundated parts (Peterken 2013) and MG8 the *Cynosurus cristatus* - *Caltha palustris* (crested dog's tail-marsh marigold), where the water table is kept higher in the summer (for example on groundwater fed systems). This definition includes non-meadow structures within floodplain meadows, such as hedgerows, unmanaged field corners and ditch banks. Geographically, this study focusses on floodplain meadows in the UK, but literature from similar grasslands in North-Western Europe is included too. With regards to effects of conservation management, studies from other grassland ecosystems (dry grasslands, salt marshes etc.) that demonstrate particular mechanisms that are likely to be important in floodplain meadows, are included as well. This study is limited to terrestrial invertebrates and, within those, focusses on 'larger' species, excluding soil meso- and microfauna such as mites and nematodes. Due to this terrestrial focus, aquatic habitats (rivers, ditches and ponds) and conservation management performed on them are not discussed. Some terrestrial invertebrates do however have aquatic immature stages (e.g. dragonflies and various dipteran taxa), making it paramount to adopt a landscape approach to floodplain-meadow management. Although these aquatic stages are not primarily included in this review, we do highlight potential aquatic needs, where they occur.

2. Methods and database

To gain an overview of all published literature on the invertebrate assemblages of North-West European floodplain meadows, literature searches were carried out in Web of Science on 16-06-2016 (see Table 1 for the exact search terms used). This resulted in a list of 58 publications falling within the scope of this study (see Appendix A). Nearly half of these studies are published in international scientific journals (27), with most others published in national zoological or taxonomical journals (28). In addition to this, the search result included one book chapter and two reports. Most studies were conducted in Germany (37), followed by the Netherlands (8), the UK (7) and Belgium (2). The search result also included two review articles based on work from various countries. The most frequently studied invertebrate groups are beetles (22, predominantly focussing on carabid beetles only), flies (10), spiders (8), molluscs (8), earthworms (8) and grasshoppers (5). Most of the articles published in national journals contained observational case-studies, rather than studies with a clear sampling design aimed at comparing habitat types, flooding regimes or management. Therefore, I have focussed primarily on the international publications, with additional sources consulted only where this was likely to add new insights. For practical reasons, studies in languages other than English, German and Dutch were excluded. A recent PhD thesis on floodplain-meadow beetles (Shepherd 2013), which did not show up in the Web of Science searches was also consulted.

Table 1. Keywords used in Web of Science searches.

Keywords
Floodplain meadow invertebrate
Floodplain meadow beetle
Floodplain meadow butterfly
Floodplain meadow hymenoptera
Floodplain meadow grasshopper
Flooded grassland invertebrate UK
Flooded grassland invertebrate Netherlands
Flooded grassland invertebrate Germany
Flooded grassland invertebrate Belgium
Flooded grassland invertebrate France
Flooded grassland invertebrate review
Floodplain meadow invertebrate review
Flooded grassland arthropod review
Floodplain meadow arthropod review

3. Arthropods associated with floodplain meadows

Floodplain meadows harbour a rich invertebrate fauna. Various German studies emphasise the species richness of floodplain meadows and high occurrence of red list species e.g. for molluscs (Foeckler et al. 2006), leafhoppers (Nickel and Hildebrandt 2003) and carabid beetles (Gerisch et al. 2012a). Maher et al. (2014) found more than one third of the Irish species of sciomyzid flies in twelve hay meadows along the river Shannon in Ireland and floodplain meadows in the UK have been recorded to be rich in phytophagous beetles (Woodcock et al. 2005; Woodcock et al. 2012) and true bugs (Morris 1990). Kalkman et al. (2003) demonstrated that 69 % of the Dutch grasshopper species are found in the floodplains along the river Rhine, along with 44-50% of the country's carabid beetle, bee, wasp, hoverfly and mollusc species. Most of these species were found in floodplain grasslands, although it is unclear how many of these grasslands comprised mown meadows.

To what extent the species composition of floodplain meadows resembles that of other, drier grasslands, differs between taxonomic groups (see also Chapter 7 for differences with grazed or fallow wet grasslands). The species composition of true bugs (Morris 1990), bees (Peeters and Nieuwenhuijsen 2012) and butterflies (Fies et al. 2016) in floodplain meadows resembles that of drier grasslands. Also with respect to soil macroinvertebrates, such as earthworms, millipedes and centipedes, the species composition of floodplain meadows is similar to non-flooding grasslands (Plum 2005). For carabid beetles and staphylinid beetles, however, the species composition in floodplain meadows is very different from that in dry grasslands (Luff et al. 1992; Shepherd 2013). The moistness of the soil seems to play an important role in shaping the species composition (Luff et al. 1992) and floodplain grasslands particularly share species with bogs, wet woodlands and wet agricultural grasslands (Turin et al. 2003). Floodplain-meadow beetle communities are nonetheless quite distinct, even compared to floodplain fen and woodland habitats (Shepherd 2013). Many hoverflies found in Dutch floodplain grasslands seem to be largely restricted to wet, open, flower rich habitats, which combine high flower abundance for adult feeding with (semi-) aquatic habitats for larval development. The species composition of floodplain meadows is most similar to that of flower-rich reed marshes, wet grasslands, wet heathlands, bogs and (wet) ruderal sites (Reemer et al. 2009). Particularly among relatively mobile invertebrates, including spiders, carabid beetles and true bugs, floodplain meadows are also home to many ruderal species.

Although floodplain meadows are relatively species rich, the number of unique species, entirely restricted to these habitats, seems limited. A comprehensive review on soil macrofauna in floodplain grasslands (Plum 2005) concluded that there are no terrestrial earthworms, potworms, snails, woodlice, millipedes or centipedes that are restricted to floodplain grasslands. Instead, these grasslands are inhabited by 'well-adapted generalist and opportunists that are favoured by flooding' (Plum 2005). Other literature sources, however, do mention some typical floodplain grassland soil macrofauna, particularly snails. The most prominent example is the Desmoulin's whorl snail (*Vertigo moulinsiana*), an EU Annex II species, which is restricted to wet calcareous grasslands and fens along rivers and lakes¹. Kalkman et al. (2003) also mentions *Pseudotrichia rubiginosa* as a typical floodplain snail for the Netherlands. Its distribution in the UK, where this species is rare and declining, also suggests a strong reliance on floodplains², although it may rely more on wooded floodplain sites, rather than meadows. Rothenbücher and Schaefer (2005) list two stenotopic leafhopper species that

are particularly prevalent in frequently flooded floodplain meadow grasslands, *Erzaleus metrius* and *Megamelus notula*. Similarly, Moller Pilot (2005) and Lehmann and Stark (2004) list a number of stenotopic floodplain meadow species of terrestrial chironomids and dolichopodid flies respectively. Drake (1998) gives a long list of invertebrate species that are nationally rare in England, but occur widely on lowland wet grasslands. This list includes a wide range of beetle and fly families as well as a large number of moths and two dragonfly species. Four rare species, one true bug (*Capsus wagneri*), one weevil (*Apion difforme*) and two click beetles (*Selatosomus angustulus* and *S. nigricornis*), seem to be completely restricted to wet grasslands in England (Drake 1998). Gerisch et al. (2006) lists 27 carabid beetle species which are strongly associated with specific flood duration and groundwater depth conditions within floodplains of the river Elbe. A comprehensive study on a range of invertebrate taxa in Dutch floodplains was conducted by Kalkman et al. (2003). They list 94 species (including 68 carabid beetle, 9 bee and 7 wasp species) for which floodplain habitats account for more than 20% of their distribution in the Netherlands (in total, floodplain-meadow habitats cover 1.3% of all 1 x 1 km-squares in the Netherlands). This list includes species found in floodplain woodlands, on dykes and on gravel banks. Only three species are mentioned as being particularly indicative of floodplain grasslands, the parasitic bee *Nomada fabriciana*, the carabid beetle *Agonum muelleri* and the hoverfly *Helophylus trivitattus* (all of which are widespread, but not very common, in the UK). This demonstrates that most of the floodplain grassland species also use other parts of the floodplain landscape for part of their life-cycle, including flower rich dykes, hedgerows, woodlands and fens.

¹ <http://jncc.defra.gov.uk/protectedsites/sacselection/species.asp?FeatureIntCode=S1016>

² <http://www.animalbase.uni-goettingen.de/zooweb/servlet/AnimalBase/home/species?id=3122>

4. Ecological impact of invertebrates in floodplain meadows

Invertebrates are a large and essential component of the floodplain meadow ecosystem. They are the largest contributor to all levels of the food web, except primary producers, certainly in terms of diversity, but in many cases also in terms of total biomass. Earthworms, woodlice, millipedes, centipedes, a proportion of the floodplain-meadow ant and beetle species and numerous fly larvae are detritivores. They decompose dead plant material and make it available again for plant growth. Herbivorous invertebrates, including grasshoppers, weevils and other beetles and butterfly and moth larvae reduce plant biomass. This can lead to increased structural heterogeneity of the vegetation sward, increased light penetration - which can benefit seed germination - and reduced dominance of competitive plant species. Invertebrate floodplain-meadow carnivores include carabid and staphylinid beetles, spiders, ants, wasps and various fly families. These species keep the number of invertebrate detritivores and herbivores under control and hence stabilise their effects on nutrient cycling and vegetation structure. In turn, invertebrates across these trophic levels, provide food for meadow birds, mammals (badger, shrews and bats), reptiles and amphibians. Earthworms and large flies like Tipulidae are bulk food for wading birds like common snipe, black-headed gull, lapwings, black-tailed godwit, redshank and oystercatcher (Plum 2005; Rhymer et al. 2010). Earthworms are also essential bulk food for badgers and little owls (Thonon and Klok 2007) and have even been found to form a large component of the diet of some wetland fish (Plum 2005).

Invertebrate pollinators, including bees, butterflies and many fly families, play a particularly important role in maintaining plant diversity in floodplain meadows. Although pollinators in floodplain meadows have received little scientific attention, their pollination services are essential to the reproduction of a wide range of floodplain meadow plant species. Theoretically, pollinators in floodplain meadows may also contribute to food production by pollinating food crops in nearby gardens, fields and orchards. This may particularly happen over distances of less than 750m (Gathmann and Tscharntke 2002; Steffan-Dewenter et al. 2013) and in crops that lack suitable nesting sites or have a flowering season that is too short to support pollinator assemblages on their own. The extent of such landscape-wide pollination services is currently unknown as concise research on the contribution of natural habitats on pollination services for food production are largely lacking (Garibaldi et al. 2014).

A final important role of invertebrates in floodplain meadows is improving soil structure and moving nutrients deeper into the soil. Earthworms in particular transport nutrients and minerals, aerate compacted soils and increase the water infiltration capacity through their extensive burying behaviour (Plum 2005). Their soil structuring capacity is particularly important for the recovery of compacted, consolidated and unstructured soils after flooding. Also ants may play an important role as ecosystem engineers by creating extensive nests with loose soil and a warm and moist microclimate. This provides favourable conditions for other species, including rare plants. Again, studies on the specific impacts of soil invertebrates in floodplain meadows are, however, lacking (Plum 2005).

5. Habitats and host species

Invertebrate species inhabit all parts of the floodplain meadow and most species inhabit different parts of the ecosystem or even different parts of the landscape throughout their life-cycle. Carabid beetles live on the ground or in the vegetation as adults, where they prey on other invertebrates or feed on plants, particularly plant seeds (Turin 2000). As larvae, most species live in the ground (Turin et al. 2003), along with, for example, earthworms and larvae of a large number of fly families (Plum 2005). Adult flies, including hoverflies, live above ground, where many species contribute to pollination. Most hoverflies found in floodplain meadows have predatory larvae (often feeding on aphids on shrubs and forbs) or aquatic larvae that feed on detritus in puddles, dung heaps and ditches (Kalkman et al. 2003). Only 12% of the syrphid species found in Dutch floodplains had phytophagous larvae, which live inside plants, where they mine leaves or roots (Kalkman et al. 2003). Bees and wasps are also important pollinators. Most species found in floodplain meadows are polylectic (73% of bee species found in Dutch floodplain meadows), feeding on a wide range of flower species (Kalkman et al. 2003). Most floodplain species nest underground (61% of bees and 35% of wasps), often on bare ground or in clay or sand cliffs. The importance of small cliffs in floodplain meadows for ground nesting bees is highlighted by Mader and Voelkl (2002). Around a quarter of the bee and wasp species found in floodplain meadows are parasitic, laying their eggs in the nests of other bees and wasps. The remaining species nest above ground, often in hollow plant stems (e.g. bramble thickets) or other plant materials (Kalkman et al. 2003). Dragonflies, which hunt in floodplain meadows as adults, all have aquatic larvae, which, depending on the species, live in ponds, lakes, ditches, streams or rivers.

These examples all demonstrate the interdependence of different parts of the floodplain meadow ecosystem. Indeed, (Drake 1998) particularly highlights the importance of fens, water margins, standing water, isolated trees, hedges and field margins for wet grassland invertebrates. These features are not only important for the completion of specific life-stages, but also provide wetter and drier habitat, where species can take shelter during extremely dry or wet seasons. Trees and shrubs are used by some species to escape floods (Plum 2005) and the early flowering period of blackthorn, hawthorn and willow means that these species provide valuable nectar and pollen sources in early spring, when the number of flowers in the meadow is still limited (Peeters and Nieuwenhuijsen 2012). Availability of nesting sites in the form of vertical cliffs, bare ground and dead wood in flower-rich floodplain meadows can also significantly increase bee diversity and abundance (Mader and Voelkl 2002).

Variation in soil elevation and vegetation structure is also an important factor shaping invertebrate richness in floodplain meadows across a wide range of taxonomic groups (Drake 1998; Kalkman et al. 2003). Species richness of bees and wasps increased with soil elevation in a number of Dutch floodplain grasslands, while the number of carabid beetles and hoverflies decreased with soil elevation, reflecting the moisture requirements of their larval stages (Kalkman et al. 2003). Gerisch et al. (2006) report a strong effect of flood duration and groundwater depth on carabid beetle species assemblages in floodplain grasslands along the Elbe river. Small scale variation in environmental parameters is also very important for hoverfly and sciomizid fly species richness in floodplain meadows (Dziöck 2006; Maher et al. 2014). A comparison of irrigated and non-irrigated

floodplain meadows revealed that irrigation and elevated humidity affected species composition and shifted assemblages towards moisture-dependent species. However, the number of species of conservation concern, did not differ between irrigated and non-irrigated meadows and both alpha diversity (species richness and Simpson diversity) and beta diversity (multivariate homogeneity of group dispersions) of orthopterans, carabids, and spiders were not significantly different between the two (Schirmel et al. 2014). Spider densities were significantly higher in irrigated meadows.

Data on important host plant species in floodplain meadows are scarce. The biology of the few typical wet grassland species identified by (Drake 1998) is poorly known and most bee, wasp and hoverfly species with a strong representation in floodplain habitats (see (Kalkman et al. 2003) are polylectic. They feed on a wide range of flowers, including bogbean (*Menyanthes trifoliata*), bramble (*Rubus fruticosus* agg.), wild carrot (*Daucus carota*), dandelion (*Taraxacum* sp.), daisy (*Bellis perennis*), hogweed (*Heracleum sphondylium*), marigold (*Calendula* sp.), ragwort (*Senecio jacobaea*), field scabious (*Knautia arvensis*), speedwell (*Veronica* sp.), spurge (*Euphorbia* sp.), stitchwort (*Stellaria* sp.), creeping thistle (*Cirsium arvense*), yarrow (*Achillea millefolium*) and willow (*Salix* sp.)³. The two leafhopper species typical for floodplain meadows identified by Rothenbucher feed on *Phalaris arundinacea* and *Carex* spp. respectively.

³ www.bwars.com.

6. Effects of flooding on floodplain meadow invertebrates

Flood survival adaptations

Flooding is a disturbing event for terrestrial invertebrates in floodplain meadows. Yet, a number of species are well adapted to flooding events and even benefit from them, as floods reduce populations of competitors and increase the availability of certain resources (Gerisch et al. 2012a). Flood survival strategies can be divided into dispersal strategies and coping strategies. The occurrence of both types of strategies among a wide range of invertebrates are discussed by Kalkman et al. (2003) and Plum (2005). Physiological or behavioural adaptations to survive floods, at least during certain life-stages, are very common among soil invertebrates, which are generally more tolerant to inundation than to drought (Plum 2005). Specific adaptations have been reported for earthworms, potworms, chilopods and dipteran larvae (Plum 2005) and for bees, wasps, carabid beetles, molluscs, grasshoppers and hoverflies (Kalkman et al. 2003). Various soil invertebrates can survive under water as long as oxygen levels remain high, particularly in cold water (Plum 2005). Most grasshoppers and some snails are able to tolerate inundation, at least for a short time, during the egg stage and some bees and wasps build watertight chambers for their hibernating larvae (Kalkman et al. 2003). Kajzer-Bonk et al. (2013) report the survival of *Maculinea* caterpillars in ants' nests that were completely inundated during a spring flood. This implies that also (certain) ants are capable of surviving floods in their nests, which was also suggested by Lafage et al. (2015). Various adult carabid beetles can also survive periods of inundation either through physiological adaptations, or by trapping air bubbles under water (Kolesnikov et al. 2012).

Flood survival through dispersal includes horizontal dispersal, where soil invertebrates move to more aerated soil layers, and vertical dispersal to nearby higher ground (Plum 2005). Larger, mobile species, including many adult carabid beetles, spiders, grasshoppers, bees, wasps and flies can move to higher ground and quickly recolonize floodplain meadows after the floodwaters have receded (Kalkman et al. 2003; Plum 2005). Higher ground also provides essential refuge sites for terrestrial chironomid flies (Moller Pilot 2005). Hedgerows and other higher structures can form important refuge sites within the meadow, from which spiders (Lafage et al. 2015) as well as woodlice, diplopods and earthworms (Plum 2005) can recolonize floodplain meadows. Snails can survive floods by climbing onto floating vegetation (Plum 2005). This also provides an excellent dispersal strategy, enabling rapid recolonization, even for species with poor intrinsic mobility. Winter floods can also be evaded by species with distinct life stages, including bumblebees, which have colonies within the meadow in summer, but hibernate elsewhere as single queens (Kalkman et al. 2003).

Population level effects of flooding

The effect of flooding on invertebrate populations differs not only between species, but also highly depends on the season and flood duration. A meta-analysis of flooding effects on soil invertebrates found that both increases and decreases in abundance and/or diversity have been recorded for earthworms, snails, woodlice, diplopods, centipedes and dipteran larvae (Plum 2005). Earthworms, snails and isopods were most abundant in floodplains that flooded for less than 4 months each winter or every second winter. Extensive winter flooding and summer floods dramatically reduced earthworm, woodlice, centipede and diplopod abundances. Flooding also alters the species composition of soil invertebrates (Plum 2005), as some species are better adapted to survive

prolonged inundation (Zorn et al. 2008; De Lange et al. 2013). The impact of summer flooding on earthworms was also shown to depend on soil type and inundation duration, which affect soil oxygen levels.

Many carabid beetle species seem well adapted to winter floods, with several authors reporting higher abundance or diversity in flooding compared to non-flooding grasslands (Lessel et al. 2011; Gerisch et al. 2012a). Flooding nonetheless has a strong impact on species composition and reduces carabid beetle functional diversity (Gerisch et al. 2012a). Flooding increases prey availability (including aquatic species that are left in the floodplain after flood events) and prey accessibility (by forcing soil dwelling invertebrates towards the surface), which attracts a large number of mobile, opportunistic, predatory species. This phenomenon also explains the increased abundance of wolf spiders in regularly flooding meadows (Lafage et al. 2015). Meanwhile, flooding reduces the suitability of floodplain meadows for other carabid beetle feeding guilds.

Extreme summer floods have a very different impact on carabid communities than regular winter floods. Various studies have shown strong reductions in carabid beetle abundance and diversity directly after extreme spring and summer floods (Ilg et al. 2008; Gerisch et al. 2012b; Lafage et al. 2015). Pre-flood richness values were reached again within 2 years, although beta diversity remained relatively high, indicating persistent shifts in species composition and abundances (Gerisch et al. 2012b). Assemblages inhabiting plots prone to (winter) flooding did not recover faster than those on rarely inundated plots. This demonstrates that species that are adapted to cope with winter floods, may not be able to survive summer flooding, e.g. because they lack physiological adaptations at the larval stage or are unable to deploy behavioural adaptations during the active reproductive season. Strategies related to dispersal and habitat generality were identified to be crucial for the quick community recovery following an extreme flood (Gerisch et al. 2012b). The ability to quickly recolonize suitable habitat was also reported by (Günther and Assmann 2005), who found that many stenotopic floodplain meadow carabid beetles had reached newly created floodplain meadows within one year of creation.

Like carabid beetles, mollusc diversity peaks at intermediate flood disturbance and moisture levels (Ilg et al. 2012), but summer floods seem much less disturbing for this group. Survival rates of extreme summer floods are much higher than for carabid beetles (Ilg et al. 2008) and Ilg et al. (2009) even reported increased mollusc diversity in the first year after an extreme flood event. This was partly due to the fact that a number of aquatic species invaded the meadow. Overall, spatio-temporal habitat heterogeneity played an important role in maintaining mollusc diversity (Ilg et al. 2009).

Research by (Maher et al. 2014) on sciomyzid flies, hoverflies and plants found that flood depth and duration have a strong influence on species assemblages. Sciomyzid species richness and total abundance were both positively correlated with hydroperiod and flood depth, while both plants and syrphids responded negatively to increases. Rothenbücher and Schaefer (2005) reported that flooding reduced leafhopper species richness in fallow floodplain grasslands, but not in mown sites, which already harbour lower species numbers. In fallows that were subject to summer and winter floods, pioneer species prevailed. In contrast, in fallows that were flooded a long time during winter but not in summer, communities of very specialised species were found which were not very species-rich.

With some invertebrate species profiting from flood events, while others are negatively affected, the impact of flooding on invertebrate prey availability for birds depends on the bird's main prey species. Moreover, even when total prey biomass is reduced by flooding, prey availability may actually increase as soil invertebrates (e.g. earthworms) move to the surface (Plum 2005; Rhymer et al. 2010).

7. Impact of conservation management

The literature search revealed only eight studies on the effects of regular floodplain meadow management (or the lack thereof) on invertebrates. A small number of additional studies investigated the effects of floodplain meadow restoration (e.g. on ex-arable land) (Woodcock and McDonald 2008) or reviewed the effects of abandonment (Joyce 2014). The eight studies on effects of regular management all had a different taxonomic scope, ranging from specific families or genera (carabid beetles, snails, grasshoppers and leafhoppers) to wider groups (phytophagous beetles bird prey and various larger species groups). The compared treatments also differed between all of these studies, e.g. comparing intensive agricultural use (fertilization and multiple hay cuts per year) to more extensive use, aftermath grazing with sheep or cattle to a hay cut without aftermath grazing or investigating the effect of uncut strips in meadows with an annual hay cut.

Carabid beetles were little affected by changes in management intensity in a German floodplain. They appeared to be more sensitive to hydrology and microclimate, which were similar across management types, than to vegetation biomass (Andretzke 2002). Management intensity did alter snail species assemblages in floodplains along the Elbe river (Foeckler et al. 2006). Woodcock et al. (2005; 2008) demonstrated that aftermath grazing with cattle was more beneficial for phytophagous beetles than aftermath grazing with sheep or no aftermath grazing. However, these studies did not investigate the effect of hay cutting or benefits of leaving some strips uncut. Butterflies, true bugs, leaf beetles, weevils and dragonflies were more abundant in late mown strips than in floodplain meadows mowed in June (Handke et al. 2011). This effect was most pronounced when surrounding meadows were cut simultaneously in June. In the same study, grasshoppers and leaf beetles showed no overall preference for early or late mowing sites. These findings are in conjunction with (Waeber 2005), who demonstrated that staggering mowing dates was beneficial for grasshoppers, as different species preferred different mowing dates. Overall bird prey availability is greatly reduced by mowing (Behrens et al. 2007), although for some bird species, prey may become more accessible directly after mowing.

Rothenbücher and Schaefer (2005) compared fallow floodplain grasslands to sites receiving two hay cuts per year and found that leafhoppers responded overall negatively to hay cutting, diminishing the species assemblage to common pioneer species. Also a review by Joyce (2014) revealed that the few studies that reported effects of abandonment of floodplain meadow management on invertebrates, predominantly showed increased species richness in abandoned grasslands, particularly in the first 20 years after abandonment.

In all, these findings on the impact of floodplain meadow management on invertebrates are well aligned with evidence from other grassland systems. An extensive literature review on effects of grazing on grassland invertebrates demonstrated that although some form of management is required to prevent succession to woodland, intensive grazing is detrimental (van Klink et al. 2015). Effects of grazing were shown to vary considerably among invertebrate groups, but overall invertebrates proved to be much more sensitive to grazing than plants. An analysis of underlying mechanisms revealed that grazing is most beneficial when it increases variation in vegetation structure and microclimate without considerably impacting on food availability or causing direct

disturbance and mortality (van Klink et al. 2015). Mowing in essence resembles a bout of quick, intensive grazing (but without additional nutrient input), increasing its potential for direct disturbance and decreasing vegetation structure and variation in microclimate. Mowing can therefore be expected to have a negative impact on species living in the vegetation layer at the time of mowing, which has indeed been demonstrated for various invertebrate groups, including grasshoppers (Humbert et al. 2010a) and butterflies (Dover et al. 2010). This negative impact can (partly) be mitigated by leaving strips uncut or by staggering mowing dates among adjacent fields and by mowing towards unmown field sections (Humbert et al. 2009; Humbert et al. 2010b; Humbert et al. 2012). Some types of mowing equipment are also more insect friendly than others (Humbert et al. 2009; Humbert et al. 2010b). Such mitigation is only effective if mowing occurs when species are mobile (adult, non hibernating stages) and should therefore not be left too late (van Noordwijk et al. 2012). Late mowing may be effective for species hibernating in the ground, in water bodies or outside the meadow. Best overall results can be expected from a landscape approach where management dates vary among a set of adjacent meadows (Humbert et al. 2009; van Klink et al. 2015), ensuring continuous availability of cover and food.

8. Conclusions and recommendations

- Invertebrates in floodplain meadows are strongly understudied compared to plants. Only a handful of studies on floodplain invertebrates has been carried out in the UK and even when all studies from North-Western Europe are pooled, many questions remain on species affinity to floodplain meadows, their life-cycles, habitat use and their response to flooding and conservation management. Carabid beetles, spiders, molluscs and earthworms have received most attention, while, for example, bees, wasps and butterflies, which perform important ecosystem services as pollinators, have hardly been studied.
- Floodplain meadows harbour a rich invertebrate fauna that is distinctively different from other grassland types. Typical floodplain meadow invertebrates include general grassland species, attracted by the great diversity of plant species, hydrophyllous species, that depend on the high soil moisture levels (particularly for their larval stages) and opportunistic pioneer species that profit from the changes in food availability and competition caused by the flood dynamics. Only few species are strictly limited to floodplain meadows, but this does not mean that floodplain meadows are unimportant for invertebrates. On the contrary, floodplain meadows are an essential landscape component for many invertebrates and an important stronghold for species typical of (wet) flower-rich grasslands, which have declined strongly over the last century.
- Invertebrates play a number of important roles within the floodplain meadow ecosystem as decomposers, herbivores, carnivores and pollinators. Soil macroinvertebrates are essential for structuring and aerating the soil and for moving nutrients deeper into the soil. Invertebrates are also essential food for wading birds, mammals, amphibians and reptiles.
- Invertebrate diversity in floodplain meadows depends highly on habitat diversity. Different species favour different soil elevation and inundation levels and the presence of a range of conditions creates refuge sites during extremely wet or dry events. Features such as fens, water margins, ditches, hedgerows, vertical cliffs and bare soil are hugely important for invertebrates as many species need a combination of different microhabitats to complete their life-cycle. Some species even depend on more than one habitat type to complete their life-cycle, highlighting the need for a landscape approach to floodplain meadow conservation.
- A large number of floodplain meadow invertebrates has physiological or behavioural adaptations to survive flood events. Many carabid beetles, bees, wasps, molluscs, earthworms and flies are able to survive prolonged periods of inundation, particularly in winter. Moderate winter flooding may actually increase both diversity and abundance of a number of invertebrate taxa. Spring and summer flooding generally have a negative impact on invertebrate diversity and abundance, but most populations recover within a few years, even after extremely devastating flood events. Nearby higher ground, including trees and hedgerows within the meadow are important refuge sites to ensure quick recolonization after flood events.
- Effects of traditional hay meadow management on invertebrates in floodplains have been little studied, but the few studies so far indicate that hay cutting across an entire field has a devastating effect on invertebrates living in and on the vegetation, including butterflies, true bugs, leafhoppers, weevils and dragonflies. Soil invertebrates and ground dwelling species,

including carabid beetles, are less affected by mowing management (but may still be affected by changes in microclimate due to the reduction in vegetation cover). In the long term, some form of mowing or grazing management is essential to preserve an open vegetation structure and to prevent shrub and tree encroachment, but, similar to other grassland habitats, invertebrates seem more sensitive to over-management of floodplain meadows than plants. Late mowing (in August or September rather than June) is often suggested as a less destructive alternative. However, the only study comparing the effect of different mowing dates in floodplain meadows found that late mowing was particularly beneficial if surrounding land was cut in June, indicating that a variety of mowing dates is important rather than late mowing per se. Moreover, early mowing is essential for some species and late mowing may have less favourable effects on the vegetation. As in other grassland systems, best results are expected from rotational management in which adjacent fields, or even parts of fields, are mown at different times of the year. Mowing towards unmown sections rather than mowing from the outside to the inside of a field can further enhance the survival chances of vegetation dwelling invertebrates, as can the use of more insect friendly mowing equipment. Leaving strips uncut for a year may also benefit invertebrates, but if the same strip is left uncut for consecutive years it will develop into thicket and lose its meadow species. Such thickets can in themselves be valuable parts of the floodplain meadow ecosystem, but are unsuitable to mitigate negative impacts of mowing management on grassland species. The conservation of varied meadow habitats as well as features, such as ditches, fens and hedgerows should in itself be an important management goal to enhance invertebrate biodiversity.

- The effects of aftermath grazing has only been studied for phytophagous beetles, which responded best to aftermath grazing with cattle (rather than with sheep or no aftermath grazing). Cattle may create valuable bare ground patches, but further studies are needed to establish effects on other invertebrate species and under other conditions.
- Further research is welcome on nearly all aspects of floodplain meadow invertebrate communities, but possibly the most pressing questions remain in relation to floodplain meadow management. Thorough investigation into the effects of rotational mowing, the required recovery time between mowing dates and the spatial scale at which rotational management is most effective is paramount to the conservation of floodplain meadow invertebrate communities.

RESPONSE TO STATEMENTS IN FPM BULLETIN

- 1) No invertebrate species are truly typical of floodplain meadows, they all occur in other grassland ecosystems as well.

There are a few highly specialised species that are almost entirely restricted to floodplain meadows, but the majority of species also occur in other grassland types or other wet habitats. The species composition of floodplain meadows is however quite distinctive.

- 2) Effects of management regimes on invertebrates are irrelevant because most species rely on recolonization to maintain healthy populations anyway.

A significant number of invertebrates living in floodplain have physiological or behavioural adaptations to survive periods of inundations and live in floodplain meadows throughout their life-cycle. Moreover, even species that survive floods outside floodplain meadows may heavily depend on these habitats during certain life stages and hence certain periods of the year. Instating a management regime that is not detrimental for invertebrates is therefore paramount for the survival of local populations of all these species.

- 3) Regular flooding makes fpm unsuitable as permanent habitat for invertebrates.

Many species are able to survive regular winter flooding, with numerous species boasting physiological adaptations to survive in inundated soils. Most populations even recover within a few years from extreme summer floods, which they survive by evading to higher ground, including trees and shrubs within floodplain meadow.

9. References

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Appendix 1.

Results Web of Science literature search.

Record 1 of 58

By: Andretzke, H (Andretzke, H)

Book Group Author(s): DEUT GESELL ALLGEMEINE & ANGEWANDTE ENTOMOLOG

Title: Influence of inundation on the carabid fauna of a northern German grassland area.

Source: COMMUNICATIONS OF THE GERMAN SOCIETY FOR GENERAL AND APPLIED ENTOMOLOGY, VOL 9 NO 4-6, SEPTEMBER 1995

Book Series Title: MITTEILUNGEN DER DEUTSCHEN GESELLSCHAFT FUR ALLGEMEINE UND ANGEWANDTE ENTOMOLOGIE

Volume: 9

Issue: 4-6

Pages: 813-818

Published: 1995

Conference Title: 9th Conference of the Deutschen-Gesellschaft-fur-Allgemeine-und-Angewandte-Entomologie

Conference Date: MAR 23-27, 1993

Conference Location: JENA, GERMANY

Sponsor(s): Deut Gesell Allgemeine & Angewandte Entomol

Accession Number: WOS:A1995BE99D00059

Record 2 of 58

By: Andretzke, Hartmut

Title: Evaluating the success of nature conservation measures in the wetlands of the river Wuemme near Bremen based on the carabid fauna.

Foreign Title: Erfolgskontrolle von Naturschutzmassnahmen in der Wuemmeniederung bei Bremen anhand der Carabidenfauna.

Source: Angewandte Carabidologie

Volume: 4-5

Pages: 3-17

Published: 2002

Accession Number: ZOOREC:ZOOR14005032178

Record 3 of 58

By: Armbruster, Jost

Title: [On the importance of stream restoration for the grasshopper fauna of stream flood plains.]

Foreign Title: Zur Bedeutung der Fliessgewaesser-Renaturierungen fuer die Heuschreckenfauna von Bachauen.

Source: Articulata

Volume: 17

Issue: 2

Pages: 79-87

Published: 2002

Accession Number: ZOOREC:ZOOR13900021056

Record 4 of 58

By: Barendregt, Aat; Prijs, Joop; Velterop, Jan

Title: Snail-killing flies of the genus *Anticheta* in the Netherlands, with two species new to the fauna (Diptera: Sciomyzidae).

Foreign Title: Slakkendodende vliegen van het genus *Anticheta* in nederland, met twee soorten nieuw voor de fauna (diptera: Sciomyzidae).

Source: Nederlandse Faunistische Mededelingen

Volume: 42

Pages: 47-54

Published: Jul 15 2014

Accession Number: ZOOREC:ZOOR15010058440

Record 5 of 58

By: Behrens, Martin; Artmeyer, Christoph; Stelzig, Volker

Title: Food resources for meadow birds in wet grassland - Management effects and consequences for bird protection

Source: Naturschutz und Landschaftsplanung

Volume: 39

Issue: 11

Pages: 346-352

Published: NOV 2007

Accession Number: BCI:BCI200800065874

Record 6 of 58

By: Beylich, Anneke; Graefe, Ulfert

Title: Investigations on the enchytraeid fauna in floodplain soils of the Lower Middle Elbe.

Source: Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis Biologia

Volume: 110

Pages: 107-122

Published: 2007(2008)

Accession Number: ZOOREC:ZOOR14503016382

Record 7 of 58

By: Bradbury, RB (Bradbury, Richard B.); Kirby, WB (Kirby, Will B.)

Title: Farmland birds and resource protection in the UK: Cross-cutting solutions for multi-functional farming?
Source: BIOLOGICAL CONSERVATION
Volume: 129
Issue: 4
Pages: 530-542
DOI: 10.1016/j.biocon.2005.11.020
Published: MAY 2006
Accession Number: WOS:000237878900010

Record 8 of 58
By: Dauber, Jens
Title: Ants in meadows and reeds of the Rhine river corridor close to Guntersblum (Rhineland-Palatinate).
Foreign Title: Die Ameisenfauna (Hymenoptera: Formicidae) des Unterfeldes bei Guntersblum.
Source: Mainzer Naturwissenschaftliches Archiv Beiheft
Volume: 30
Pages: 115-119
Published: 2007
Accession Number: ZOOREC:ZOOR14307048050

Record 9 of 58
By: De Lange, HJ (De Lange, H. J.); Kramer, K (Kramer, K.); Faber, JH (Faber, J. H.)
Title: Two approaches using traits to assess ecological resilience: A case study on earthworm communities
Source: BASIC AND APPLIED ECOLOGY
Volume: 14
Issue: 1
Pages: 64-73
DOI: 10.1016/j.baae.2012.10.009
Published: 2013
Accession Number: WOS:000317321300008

Record 10 of 58
By: Drake, M (Drake, M)
Edited by: Joyce, CB (Joyce, CB); Wade, PM (Wade, PM)
Title: The important habitats and characteristic rare invertebrates of lowland wet grassland in England
Source: EUROPEAN WET GRASSLANDS
Book Series Title: LANDSCAPE ECOLOGY SERIES
Pages: 137-149
Published: 1998
Accession Number: CCC:000075298500009

Record 11 of 58
By: Dziock, F (Dziock, Frank)
Title: Life-history data in bioindication procedures, using the example of hoverflies (Diptera, syrphidae) in the Elbe floodplain
Source: INTERNATIONAL REVIEW OF HYDROBIOLOGY
Volume: 91
Issue: 4
Pages: 341-363
DOI: 10.1002/iroh.200510889
Published: 2006
Accession Number: WOS:000240231900006

Record 12 of 58
By: Foeckler, F (Foeckler, Francis); Deichner, O (Deichner, Oskar); Schmidt, H (Schmidt, Hans); Castella, E (Castella, Emmanuel)
Title: Suitability of molluscs as bioindicators for meadow- and flood-channels of the elbe-floodplains
Source: INTERNATIONAL REVIEW OF HYDROBIOLOGY
Volume: 91
Issue: 4
Pages: 314-325
DOI: 10.1002/iroh.200610887
Published: 2006
Accession Number: WOS:000240231900004

Record 13 of 58
By: Follner, K (Follner, Klaus); Henle, K (Henle, Klaus)
Title: The performance of plants, molluscs, and carabid beetles as indicators of hydrological conditions in floodplain grasslands
Source: INTERNATIONAL REVIEW OF HYDROBIOLOGY
Volume: 91
Issue: 4
Pages: 364-379
DOI: 10.1002/iroh.200510890
Published: 2006
Accession Number: WOS:000240231900007

Record 14 of 58
By: Gerisch, M (Gerisch, Michael)
Title: Non-random patterns of functional redundancy revealed in ground beetle communities facing an extreme flood event

Source: FUNCTIONAL ECOLOGY
Volume: 28
Issue: 6
Pages: 1504-1512
DOI: 10.1111/1365-2435.12272
Published: DEC 2014
Accession Number: WOS:000344592000019

Record 15 of 58

By: Gerisch, M (Gerisch, Michael); Agostinelli, V (Agostinelli, Veronica); Henle, K (Henle, Klaus); Dziock, F (Dziock, Frank)
Title: More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity
Source: OIKOS
Volume: 121
Issue: 4
Pages: 508-515
DOI: 10.1111/j.1600-0706.2011.19749.x
Published: APR 2012
Accession Number: WOS:000301537200004

Record 16 of 58

By: Gerisch, M (Gerisch, Michael); Dziock, F (Dziock, Frank); Schanowski, A (Schanowski, Arno); Ilg, C (Ilg, Christiane); Henle, K (Henle, Klaus)
Title: Community resilience following extreme disturbances: The response of ground beetles to a severe summer flood in a Central European lowland stream
Source: RIVER RESEARCH AND APPLICATIONS
Volume: 28
Issue: 1
Pages: 81-92
DOI: 10.1002/rra.1438
Published: JAN 2012
Accession Number: WOS:000298797800008

Record 17 of 58

By: Gerisch, M (Gerisch, Michael); Schanowski, A (Schanowski, Arno); Figura, W (Figura, Wolfgang); Gerken, B (Gerken, Bernd); Dziock, F (Dziock, Frank); Henle, K (Henle, Klaus)
Title: Carabid beetles (Coleoptera, carabidae) as indicators of hydrological site conditions in floodplain grasslands
Source: INTERNATIONAL REVIEW OF HYDROBIOLOGY
Volume: 91
Issue: 4
Pages: 326-340
DOI: 10.1002/iroh.200610888
Published: 2006
Accession Number: WOS:000240231900005

Record 18 of 58

By: Guenther, Jens; Assmann, Thorsten
Title: Restoration ecology meets carabidology: effects of floodplain restitution on ground beetles (Coleoptera, Carabidae).
Source: Biodiversity and Conservation
Volume: 14
Issue: 7
Pages: 1583-1606
Published: June 2005
Accession Number: ZOOREC:ZOOR14110058868

Record 19 of 58

By: Handke, Klaus; Otte, Annette; Donath, Tobias W.
Title: Late Mowed Stripes of Grassland Promote Invertebrates in Floodplain Meadows - Results from the nature reserve "Kuhkopf-Knoblochsau"
Foreign Title: Alternierend spat gemachte Altgrasstreifen fordern die Wirbellosenfauna in Auenwiesen Ergebnisse aus dem NSG "Kuhkopf-Knoblochsau"
Source: Naturschutz und Landschaftsplanung
Volume: 43
Issue: 9
Pages: 280-288
Published: SEP 2011
Accession Number: BCI:BCI201100703925

Record 20 of 58

By: Hellenthal, Marlene; Ssymank, Axel
Title: Hoverflies (Diptera, Syrphidae) in the valley of the Wahnbach (Northrhine-Westfalia [Northrhine-Westphalia], Germany).
Foreign Title: Schwebfliegen (Diptera, Syrphidae) des Wahnbachtals im Bergischen Land (Nordrheinwestfalen, Deutschland).
Source: Volucella
Volume: 8
Pages: 219-236
Published: 20 April 2007
Accession Number: ZOOREC:ZOOR14308052615

Record 21 of 58

By: Ilg, C (Ilg, C.); Foeckler, F (Foeckler, F.); Deichner, O (Deichner, O.); Henle, K (Henle, K.)
Title: HYDROLOGICAL GRADIENT AND SPECIES TRAITS EXPLAIN GASTROPOD DIVERSITY IN FLOODPLAIN GRASSLANDS
Source: RIVER RESEARCH AND APPLICATIONS
Volume: 28
Issue: 10
Pages: 1620-1629
DOI: 10.1002/rra.1552
Published: DEC 2012
Accession Number: WOS:000312651000003

Record 22 of 58

By: Ilg, C (Ilg, Christiane); Foeckler, F (Foeckler, Francis); Deichner, O (Deichner, Oskar); Henle, K (Henle, Klaus)
Title: Extreme flood events favour floodplain mollusc diversity
Source: HYDROBIOLOGIA
Volume: 621
Pages: 63-73
DOI: 10.1007/s10750-008-9632-5
Published: MAR 2009
Accession Number: WOS:000262172000005

Record 23 of 58

By: Ilg, C (Ilg, Christiane); Dziock, F (Dziock, Frank); Foeckler, F (Foeckler, Francis); Follner, K (Follner, Klaus); Gerisch, M (Gerisch, Michael); Glaeser, J (Glaeser, Judith); Rink, A (Rink, Anke); Schanowski, A (Schanowski, Arno); Scholz, M (Scholz, Mathias); Deichner, O (Deichner, Oskar); Henle, K (Henle, Klaus)
Title: Long-term reactions of plants and macroinvertebrates to extreme floods in floodplain grasslands
Source: ECOLOGY
Volume: 89
Issue: 9
Pages: 2392-2398
DOI: 10.1890/08-0528.1
Published: SEP 2008
Accession Number: WOS:000259259300004
PubMed ID: 18831159

Record 24 of 58

By: Joyce, CB (Joyce, Chris B.)
Title: Ecological consequences and restoration potential of abandoned wet grasslands
Source: ECOLOGICAL ENGINEERING
Volume: 66
Pages: 91-102
DOI: 10.1016/j.ecoleng.2013.05.008
Published: MAY 2014
Accession Number: WOS:000336445800011

Record 25 of 58

By: Lafage, D (Lafage, Denis); Sibelle, C (Sibelle, Charlotte); Secondi, J (Secondi, Jean); Canard, A (Canard, Alain); Petillon, J (Petillon, Julien)
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Source: ECOHYDROLOGY
Volume: 8
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Pages: 1584-1599
DOI: 10.1002/eco.1606
Published: DEC 2015
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Foreign Title: De arachnofauna van alluviale graslanden langsheen de Bovenschelde: gemeenschappen na habitattherstel en suggesties voor beheer.
Source: Nieuwsbrief van de Belgische Arachnologische Vereniging
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Foreign Title: Fruehjahrsbesiedlung eines im Winter ueberfluteten Nasspolders durch Laufkafer und Spinnen im Nationalpark Unteres Odertal.
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Issue: 100
Special Issue: SI
Pages: 421-446
DOI: 10.3897/zookeys.100.1538
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Foreign Title: Flussyredynamisierung - Eine Chance fuer Wildbienen (Hymenoptera, Aculeata, Apoidea).
Source: Artenschutzreport
Volume: 12
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Accession Number: ZOOREC:ZOOR13900035570

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Source: JOURNAL OF INSECT CONSERVATION
Volume: 18
Issue: 2
Pages: 267-282
DOI: 10.1007/s10841-014-9630-z
Published: APR 2014
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Foreign Title: Zur epigaeischen Arthropodenfauna von landwirtschaftlichen Nutzflaechen der Unstrutae im Thueringer Becken Teil 1: Webspinnen und Weberknechte (Arachnida: Araneae et Opiliones)
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Issue: 2
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Foreign Title: Invloed van inundatie van graslanden op terrestrische dansmuggen (Diptera: Chironomidae).
Source: Nederlandse Faunistische Mededelingen
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Source: AGRICULTURE ECOSYSTEMS & ENVIRONMENT
Volume: 98
Issue: 1-3
Pages: 183-199
DOI: 10.1016/S0167-8809(03)00080-X
Published: SEP 2003
Accession Number: WOS:000185579900013

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Title: Wolf spiders in a vegetation gradient in the river foreland Millingerwaard.
Foreign Title: Wolfspinnen in een vegetatiegradient in de Millingerwaard.
Source: Levende Natuur
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Foreign Title: Zur epigaeischen Arthropodenfauna von landwirtschaftlichen Nutzflaechen der Unstrutaue im Thueringer Becken. Teil 2: Kaefer (Insecta: Coleoptera)

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Volume: 25
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Source: PEDOBIOLOGIA
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Foreign Title: Schwebfliegen (Diptera, Syrphidae) in der Urdenbacher Kaempe bei Duesseldorf.
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Foreign Title: Het voorkomen van loopkevers (Coleoptera: Carabidae) langs een vegetatiegradient in de Millingerwaard
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Foreign Title: Erfolgskontrolle von Pflege- und Optimierungsmaßnahmen im Wiesmet, einem Wiesenbrüter-Schutzgebiet an der Altmuehl in Nordbayern.
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Volume: 4
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Published: 1986
Accession Number: BCI:BCI198783053012