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Too complex to fail? Taxonomic and functional re-organization of ground beetle communities (*Coleoptera, Carabidae*) following an extreme flood event

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# Too complex to fail? Taxonomic and functional re-organization of ground beetle communities (Coleoptera, Carabidae) following an extreme flood event

Von der Fakultät für Biowissenschaften, Pharmazie und Psychologie der Universität Leipzig genehmigte

# DISSERTATION

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# Too complex to fail?

Taxonomic and functional re-organization of ground beetle communities (Coleoptera, Carabidae) following an extreme flood event

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#### **Dissertation** Michael Gerisch

140 Seiten206 Literaturangaben18 Abbildungen10 Tabellen6 Anhänge

# Referat

Das vermehrte Auftreten extremer Wettereignisse stellt weltweit eine der größten Gefährdungspotenziale für Biodiversität im 21. Jahrhundert dar. Bisher ist jedoch nur unzureichend bekannt, wie ökologische Systeme auf Extremereignisse reagieren.

Im Jahr 2002 trat das höchste Hochwasser seit über 100 Jahren an der Mittlere Elbe in Sachsen-Anhalt auf. Die vorliegende Dissertation beschreibt die Auswirkungen dieses Jahrhunderthochwassers auf Laufkäfer, sowie ökologische und funktionale Mechanismen, die die Resistenz bzw. Resilienz der Artengemeinschaften steuern.

Hauptergebnis dieser Arbeit ist die geringe Resistenz und die hohe Resilienz der Laufkäfer gegenüber dem Extremhochwasser, wobei einem massiven Arten- und Individuenverlust eine rasche Reorganisation der funktional-ökologischen Strukturen folgte. Dafür waren vor allem die hohe Mobilität und die Habitatgeneralität vieler Arten verantwortlich. Es konnte nicht nachgewiesen werden, dass funktionale Redundanz die Effekte von Extremereignissen kompensieren kann.

Die Resultate zeigen, dass (1) biologisch-ökologische Anpassungen an reguläre Hochwasser auch die Effekte von aperiodischen Extremereignissen kompensieren können, (2) ein temporäres Zusammenbrechen der Artengemeinschaften als Kompromiss für Biodiversität in hochdynamischen Lebensräumen dient und (3) Extremereignisse langfristig vor allem Habitatspezialisten fördern. Die Arbeit zeigt aber auch, dass ein Zunehmen der Frequenz von Extremereignissen diese Mechanismen potenziell ausschalten kann, vor allem wenn die Regenerationszeit vieler Arten unterschritten wird.



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Summary	6
Zusammenfassung	8
Chapter One General introduction Biodiversity effects of extreme events Functional biodiversity research Research objects: ground beetles in floodplains Purpose and structure of the dissertation Study area & general methodology	10 12 13 15 16
Chapter Two Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream	20
Chapter Three Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles	45
Chapter Four More species, but all do the same – Contrasting effects of ground beetle species and functional diversity to flood disturbance	68
Chapter Five Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood	88
Chapter Six Synopsis	112
Bibliography	118
List of figures	131
List of tables	132
Curriculum Vitae	133
Publications	135
<b>Oral presentations</b>	137

#### Summary

In the course of ongoing climate change, abrupt weather extremes are predicted to increase in magnitude and frequency, which is considered a major threat to biodiversity in the 21st century. Nevertheless, there are tremendous gaps in the knowledge of how biodiversity can cope with such conditions and which mechanisms exist to ensure biodiversity functioning even after extreme disturbances. The purpose of this dissertation is to gain a better understanding of the ecological mechanisms governing resilience and resistance strategies of biodiversity in response to extreme events.

In 2002, the Elbe River in Central Germany experienced severe flooding which was extreme in its intensity, spatial dimension, and timing. Using ground beetles as model organisms, this dissertation pursued three main aims:

- (a) To evaluate how rapidly species richness and diversity recovered, and how long the recovery process lagged behind the extreme flood event.
- (b) To identify the relationships between flood disturbance and species survival strategies in fluctuating environments.
- (c) To estimate the role of functional diversity for ground beetle resilience after flood disturbance.

The main hypothesis was that ground beetles were severely affected by the flood in terms of their community structure, but quickly recovered to pre-flood conditions due to their life history and physiological adaptations to floodplain dynamics. Their high resilience was expected to be driven mainly by high functional diversity and high amounts of functional redundancy in the communities.

This dissertation study was conducted in the Biosphere Reserve Middle Elbe, Germany. Ground beetle abundance and environmental data originate from two large floodplain ecology projects, and were collected from 1998 until 1999, and from 2002 until 2006 based on a highly standardized sampling scheme. Biological characteristics of the species were collected on the basis of a systematic review of the literature and stored in a database. Data analysis was done using a comprehensive set of modern uni- and multivariate techniques, making it possible to account for the variability and for the autocorrelation typically found in long-term data.

The main result emerging from this thesis is the high taxonomical and functional resilience of ground beetles, after they were massively reduced by an extreme flood event. We found that post-flood resilience of ground beetles depends on high mobility and habitat generality of the species. Habitat specialists took longer to re-establish because priority effects of early-arriving species impeded their recovery. Trait homogenization was found to be an effective strategy for coping with regular flooding: on frequently flooded sites most of the species were characterized by spring reproduction, small body size, and fully developed wings. However, there was no evidence that this functional redundancy can ensure community functioning in the course of extreme flood events.

The results provide evidence that different mechanisms contributed on various response to the maintenance of ground beetle functioning, even after extreme floods, such as pre-adaptions to regular flooding. Although species do bear the risk of complete breakdown, this thesis shows that the effects of extreme floods are compensated by the high dispersal capacity and high reproduction rate of the species, i.e. by their high re-colonization power. *Being functionally* equivalent meant that many species were affected in the same way during extreme floods, but this is regarded as a trade-off for maintaining functioning in an alternating ecosystem. Ultimately, *habitat specialists* took longer to recover from the flood, but they were found to be more competitive during regular flooding. This implies that although the immediate effects can be massive, extreme floods are merely a risk that species bear in fluctuating, stochastic environments, especially during evolutionary time scales. I therefore conclude that the extreme Elbe flood of 2002 had no major impacts on ground beetle composition and functioning on a long-term scale. However, this conclusion may no longer apply if the time needed for ecological systems to regenerate exceeds the intervals between extreme events. Currently it is not clear how organisms would adapt to such conditions, which is why research on the capacity of ecological systems to buffer extreme event effects should be fostered. More effort has also to be put into estimating the role changing biodiversity plays in the functioning of ecological systems, especially under rapidly changing conditions.

# Zusammenfassung

Im Zuge des andauernden Klimawandels werden auch die Frequenz und die Intensität extremer Wetterereignisse zunehmen. Dies stellt weltweit eine der stärksten Gefährdungsursachen für Biodiversität im 21. Jahrhundert dar. Trotzdem existieren noch immer enorme Wissenslücken bezüglich der Reaktion von Arten und Artengemeinschaften auf Extremereignisse und über die Mechanismen, die ein Funktionieren ökologischer System auch unter solchen Bedingungen ermöglichen. Wesentliches Ziel dieser Dissertation ist ein besseres Verständnis zu gewinnen, wie ökologische Prozesse und Wirkmechanismen die Resilienz und Resistenz von Biodiversität gegenüber Extremereignissen sicherstellen.

Im Jahr 2002 traten an der Elbe in Mitteldeutschland Überschwemmungsereignisse auf, die aufgrund der Intensität, der räumlichen Ausdehnung und des Zeitpunktes des Eintreffens als extrem zu bezeichnen sind. Um die Effekte dieser Flut nachzuweisen wurden Laufkäfer als Modellorganismen genutzt und folgende Hauptziele verfolgt:

- (a) Untersuchung der Reaktion von Artenreichtum und -diversität auf das Extremhochwasser und wodurch die Reorganisation der Artengemeinschaften verzögert wurde
- (b) Identifizierung der Beziehungen zwischen Überflutungsstörung und den Überlebensstrategien von Laufkäfern in Auen
- (c) Ermittlung der Rolle von funktionaler Diversität für die Resilienz von Laufkäfern nach extremen Hochwasserereignissen

Die Hauptannahme der vorliegenden Arbeit war, dass das Hochwasser die Struktur der Artengemeinschaften massiv verändert hat, diese aber aufgrund spezieller Fortpflanzungsstrategien und morphologischer Anpassungen der Arten relativ schnell wieder Vorflut-Niveau erreichte. Es wurde erwartet, dass die hohe Resilienz der Artengemeinschaften hauptsächlich durch die funktionale Diversität und ein hohes Maß an funktionaler Redundanz gesteuert wird.

Die Dissertation wurde im Biosphärenreservat "Mittlere Elbe" in Sachsen-Anhalt, Deutschland, durchgeführt. Die Daten zu Laufkäferabundanzen sowie Umweltvariablen stammen aus zwei auenökologischen Projekten und wurden zwischen 1998 und 1999, sowie zwischen 2002 und 2006 auf Basis eines standardisierten Aufnahmeprotokolls erhoben. Die biologisch-ökologischen Eigenschaften der Arten wurden in einer intensiven Literaturstudie erhoben und in einer Datenbank gesammelt. Die Daten wurden analysiert mittels moderner uni- und multivariater Auswertemethoden, die besonders die auentypische Variabilität und die zeitliche Autokorrelationen berücksichtigen.

Hauptergebnis dieser Arbeit ist die hohe Resilienz der Laufkäfer, nachdem die Artenzahlen und die Diversität massiv durch das Extremhochwasser reduziert wurden. Es wurde bestätigt, dass die hohe Resilienz überwiegend durch die hohe Mobilität, aber auch durch die Habitatgeneralität vieler Arten bestimmt wurde. Habitatspezialisten benötigten länger zur Etablierung, weil die Auswirkungen früh besiedelnder Arten die Reorganisation vieler Populationen behinderten (priority effects). Es wird gefolgert, dass die Vereinheitlichung der biologischen Artmerkmale

eine wesentliche Strategie von Auenlaufkäfern ist, um mit regulären Hochwasserereignissen zu Recht zu kommen. In häufig überflutungsgestörten Habitaten waren die meisten Arten Frühjahrsbrüter von kleiner Körpergröße mit vollständig entwickelten Flügeln. Es gab jedoch kein Hinweis darauf, dass der hohe Anteil funktional redundanter Arten die Artengemeinschaften gegenüber extremen Hochwasserereignissen "versichern" kann.

Die Ergebnisse der vorliegenden Dissertation zeigen deutlich, dass unterschiedliche ökologische Mechanismen auf verschiedenen Wirkebenen das Funktionieren von Laufkäfergemeinschaften in Auen bestimmen. Darunter zählen insbesondere die funktionalen Anpassungen an reguläre Überflutungen, wie z.B. Flügelmorphologie und hohe Reproduktionsrate im Frühjahr. Es wird jedoch auch gezeigt, dass viele Arten das Risiko eines kompletten Zusammenbruchs ihrer Populationen tragen, vor allem wenn Hochwässer im Sommer auftreten. Der hohe Anteil biologisch-ökologisch ähnlicher Arten belegt, dass viele Arten in ähnlicher Weise von stochastischen Störungen beeinflusst werden. Daher kann funktionale Redundanz kein geeigneter Mechanismus sein kann, um extreme Störungen abzupuffern, im Gegensatz zur hohen Relevanz bei regulären Hochwasserereignissen. Es wird geschlussfolgert, dass extreme Hochwässer ohne längerfristige Konseguenzen für Auenlaufkäfer einhergehen und Habitatspezialisten langfristig sogar von Extremereignissen profitieren. Die Arbeit zeigt aber auch, dass ein Zunehmen der Frequenz von Extremereignissen diese Mechanismen potenziell ausschalten kann, vor allem wenn die Regenerationszeit vieler Arten unterschritten wird. Es ist noch immer unklar, wie ökologische Systeme auf solche Bedingungen reagieren werden, weshalb die Erforschung der Rolle sich ändernder Biodiversität für das Funktionieren von Artengemeinschaften, insbesondere unter sich schnell ändernden Bedingungen, intensiviert werden sollte.

#### CHAPTER ONE General Introduction

In August 2002, the highest flooding experienced over 100 years was recorded at the Elbe River in Germany. This had been preceded by a rare VB weather situation, in which a cold front causes an east-drifting Atlantic cyclone to divert to the south. Here, the depression is warmed up over the Mediterranean Sea, heavily loaded with moisture and diverted back to the northeast. The cyclone is then forced to ascend along the cold front, whereby it quickly cools down, leading to long periods of heavy rainfall (Mudelsee 2004).

This condition caused a rapid discharge increase in many rivers in Central Europe and also led to extremely high inundation levels in the Middle Elbe region in Germany between Dessau and Magdeburg (Bundesamt für Gewässerkunde 2002, Figure 1 & Figure 1 in Chapter two). This flood was extreme in terms of its height, its duration and its seasonal and spatial occurrence and some people even regard this event as one of Europe's biggest natural disasters in living memory (Schiermeier 2003; Petrow *et al.* 2007).



**Figure 1** Dyke inundation during the 2002 Elbe flood near Coswig, Germany. Picture: André Künzelmann, UFZ (Leipzig).

Immediately after the floodwaters receded, a project was set up to estimate the effects of this extreme flood on different taxonomical groups and to use this unique opportunity to enhance scientific understanding of biodiversity effects of extreme environmental events. The HABEX project ("Floodplain Habitats After Extreme Flood Events", Scholz *et al.* 2009) itself was a successor of

the RIVA project ("Development of a Robust Generally Applicable Indicator System for Ecological Changes in Floodplain Systems", Dziock *et al.* 2006), where the drivers of floodplain biodiversity were revealed and which served as a scientific basis for HABEX. The HABEX project was designed to boost mainly two research fields: extreme event research and functional biodiversity research. A challenging aim of this work was to combine these two fields.

The dissertation presented here is a substantial outcome of the HABEX project. It shares its main goal of gaining a better understanding of the recovery of biodiversity after extreme floods while tackling innovative fields of ecology that have recently been established as research frontiers to identify ecological and functional mechanisms that lead to the patterns we can observe in natural systems. In the following I will outline the current state of extreme event and functional biodiversity research, introduce the study objects and outline the main aims of the dissertation, finishing with an introduction to the study area and the methodological approach used to sample and analyze the data.

# **Biodiversity effects of extreme events**

Many theoretical, experimental, and increasingly also studies of natural systems show that ongoing climate change is one of the main driving forces influencing ecological systems in the 21st century (Parmesan & Yohe 2003; Thuiller *et al.* 2005; Araújo & Rahbek 2006). Besides gradually changing conditions (e.g. rising temperatures), abrupt weather extremes are predicted to increase in magnitude and frequency with severe consequences for ecological, but also societal systems (IPCC 2007; Loarie *et al.* 2009). Climate change will therefore not only cause trend effects, but also lead to an increased frequency and magnitude of severe environmental events, such as extreme storms, droughts, or floods (Jentsch, Kreyling & Beierkuhnlein 2007). Such extreme events are discrete occurrences that are distinguished from a continuous process by its abruptness, no matter whether it is recurrent, expected, or normal (Jentsch & White 2001).

Because of its overarching relevance for society, scientists across economic, environmental, and social disciplines regard extreme event research as one of the biggest future challenges (e.g. Patz *et al.* 2005; Halsnæs, Kühl & Olesen 2007; Knapp *et al.* 2008). An increasing number of studies show that it is also a frontier of current ecological research, and outline that extreme events have a number of serious implications for ecosystems (Easterling *et al.* 2000; Jentsch *et al.* 2007). They can cause massive compositional and structural changes in communities (Thibault & Brown 2008), change competitive interactions between organisms (Jentsch & Beierkuhnlein 2003) or even shift ecotone boundaries (Allen & Breshears 1998). Consequently, extreme events are able to alter the performance of entire ecological processes, for example biomass production (Ciais *et al.* 2005), and disrupt ecological networks like food webs (Carnicer *et al.* 2011). Such set-backs can pose serious threats to populations, especially when recovery time may exceed intervals between extreme events if their frequencies increase (Moreno & Møller 2011).

However, most of the knowledge is derived from experimental studies (MacGillivray & Grime 1995; Jentsch *et al.* 2007; Peñuelas *et al.* 2007), and most of these focus on plants. By nature, extreme events occur sporadically (usually once in more than 100 years), often without warning, and they usually last for only a short period of time. As a consequence, studying the biodiversity effects of extreme events in natural systems is much more tedious and in most cases there is a lack of standardized data for comparing pre- and post-event conditions (Orlowsky & Seneviratne

2011; Gerisch *et al.* 2012). Without a doubt, ecology is still in the early stages of understanding extreme event effects, and more knowledge is needed to predict the future behavior of ecological systems, for example how quickly biodiversity recovers, or which components of biodiversity are more resistant to weather extremes than others.

Especially for the latter, the functional traits of species and how they can flexibly occupy ecological niches are central to understanding the mechanisms of resilience and resistance. However, recent studies suggest that many ecological mechanisms that are predicted to allow species to cope with climate change may not be effective when severe, stochastic events increase in magnitude and frequency. This is true, for example, for phenotypic plasticity, which is the ability of species to tolerate changing conditions without increasing fitness costs, and which can enable species to quickly adapt to e.q. rising temperatures (Réale et al. 2003; Schaper et al. 2012). However, plasticity weakens if extreme events occur more frequently and it is expected that under such conditions selection will favor species that exhibit certain reproduction or behavioral strategies, thereby limiting plasticity (Moreno & Møller 2011). Species with high dispersal capacities can track changes in environmental conditions, shift their distribution range and thus colonize new habitats (Parmesan et al. 1999; Maclean et al. 2008). Increasing frequencies of extreme events, however, can turn habitats into ecological traps and a high dispersal capacity is no guarantee of successful recolonization if species are lured into a poor, disturbance-prone habitat (Van-De Pol et al. 2010; Jiquet, Brotons & Devictor 2011). This shows that extreme events can push communities to their adaptive capacity, and that they have the potential to change functional characters of communities, remove entire survival strategies from ecological systems and shape the physiology, ecology, and evolution of species (Gutschick & BassiriRad 2003).

# Functional biodiversity research

Over the last decade ecological research has shifted from explaining species diversity to understanding the functional consequences of biodiversity (Loreau 2010). With the rise of functional ecology as an individual discipline, traits based approaches are now widely used in ecology. They go beyond classical taxonomical measures, e.g. species richness, and elucidate what species do in communities and ecosystems (Petchey & Gaston 2006). A general assumption of functional ecology is that not species per se, but the number, type and distribution of functional traits are crucial for the ecosystem processes and functioning (Jax 2010). Traits characterize features of organisms, no matter whether they are morphological, physiological, demographic or life-history properties (Lavorel & Garnier 2002) and act on various levels from organisms to that of ecosystems, which leads to different views and definitions of traits. Violle et al. (2007) proposed a hierarchical framework to differentiate between traits that merely describe the character of an organism and those that interact with environmental conditions and can influence the functioning of ecological systems. Only the latter is functional in the sense that it can influence the fitness of a species via its effects on growth or reproduction and it may even have feedbacks on the environmental conditions of a habitat (e.g. amounts of nitrogen in the soil caused by nitrogen fixation plants).

The purpose of identifying the number of functional traits in communities and how species or individuals are distributed among them resulted in the rapid development of functional biodiversity research. The functional group concept is one of the oldest cornerstones, the aim of which is to

reduce complexity and better predict community behavior by classifying organisms into groups most biologically relevant for specific ecosystem processes or properties (Steneck & Dethier 1994). Prominent examples are the Raunkiær plant life forms or the feeding types of benthic stream organisms (Cummins & Klug 1979). However, a priori classification of organisms into groups reduces the content of information and depends strongly on the method of classification. Moreover, differences between the species within the groups are often neglected and abundance of species is not considered (Mason et al. 2003). Therefore, during the last decade flexible measures have been developed that aim at describing the range, dispersion, and relative abundance of traits in a given system, which is referred to as functional diversity (Walker & Langridge 2002; Mason et al. 2005; Petchey & Gaston 2007; Villéger, Mason & Mouillot 2008; Laliberté & Legendre 2010). More recently, identifying the relationships between the number of species present and the performance of specific processes and functions in ecosystems has received much attention in functional biodiversity research. This biodiversity-ecosystem functioning debate is underpinned by a variety of different theoretical hypotheses (see Naeem, Loreau & Inchausti 2002; Hubbell 2006), which all serve to better understand how processes or the functioning of systems might look for a given variation in biodiversity. In this framework, it is differentiated whether a species adds no new functional information to a system (redundant species), or whether it causes detectable changes in functional diversity. That means the concepts of species diversity and functional diversity are directly related to each other instead of being treated separately, which many ecologists see as a major step toward a more holistic understanding of ecological changes (Jax 2010; Loreau 2010).

A main assumption of traits-based approaches is that habitats provide a templet on which spatial and temporal variations of the environment act as selective forces for species traits maximizing reproduction and survival (habitat templet theory, Southwood 1988). In other words, habitat conditions filter out unsuccessful traits from the potential pool of colonists, so that species must possess appropriate functional traits to pass through these filters and join a local community (Townsend, Doledec & Scarsbrook 1997; Poff 1997). This approach is promising especially in the context of this thesis, because extreme disturbances will greatly affect the composition of both species and traits. But there are still tremendous gaps in the research on how the loss of species under such extreme conditions will alter functional diversity, and hence ecosystem processes like resistance or resilience.

# **Research objects: Ground beetles in floodplains**

Floodplains are natural areas being subject to inundation and are established on fluviatile sediments of its associated rivers, with which they form an inseparable unit (Brunotte *et al.* 2009). Floodplains are amongst the most complex and species-rich ecological systems in Europe (Tockner & Stanford 2002) and are often considered as hotspots of biodiversity. However, most of the European floodplains were anthropogenically modified, so that for example in Germany only 20 % of active floodplains remained (Scholz *et al.* 2005). This ultimately led to increasing research, conservation, and restoration efforts in floodplains during the last 30 years, with high relevance not only for natural sciences, but also for social and economic fields (Moss & Monstadt 2008).

Natural changes of different kinds, such as hydrological, geomorphological, land-use, and also ecological changes, are the main characterizing elements of these ecosystems. Depending on the topographical character, elevation, proximity to groundwater and propensity for flooding,

floodplains are composed of a mosaic of spatially and temporally changing local characteristics, causing great differences in the composition, richness and diversity of plant and animal species. Disturbance is one of the most important factors shaping the biological diversity of floodplains (Ward 1998; Adis & Junk 2002) and there are a number of studies which estimate the effect of flood disturbance on plant and animal communities (Amoros & Bornette 2002; Renofalt, Nilsson & Jansson 2005; Lepori & Malmqvist 2007). Flow variation drives erosion and sedimentation, which in turn interrupt the succession of species communities and create new surfaces for colonization. The periodic change of floods and droughts, and especially that of extreme floods, resets the "ecological clock" and restores communities that would disappear in a less disturbed environment. It is also these dynamics that cause the alluvial flora and fauna to display a large range of resistance and resilience strategies, based on special life-history, behavioral, and morphological adaptations to survive in these fluctuating environments (Lytle & Poff 2004).

This is also true of ground beetles (Coleoptera, Carabidae), which are one of the most speciesrich, abundant, and best studied macroinvertebrate group in floodplains. Ground beetles were used as model organisms in this dissertation for many reasons. First, understanding ground beetle occurrence in floodplains has a long tradition and several studies report on the effects of regular and periodic flooding on ground beetles (e.g. Greenwood, Bickerton & Petts 1995; Bell, Petts & Sadler 1999; Bonn, Hagen & Reiche 2002; Sadler, Bell & Fowles 2004; Lambeets et al. 2008). Overall, these studies outline the high resilience of floodplain ground beetles to regular, periodic floods, as most of these species use a "risk strategy", combining high reproduction, dispersal and remigration rates following disturbances (Zulka 1994; Adis & Junk 2002). Second, there is quite a good understanding of basic ecological mechanisms that enable ground beetles to survive and assemble in floodplains. Most of the species are good flyers, which allows to actively evade rising floodwaters and to quickly recolonize the habitats after flooding (Desender 1989). Many floodplain species are habitat generalists (Weigmann & Wohlgemuth-von Reiche 1999), which increases their ability to guickly recolonize habitats after flooding. Moreover, adults of several ground beetles can stay submerged for a considerable time period and are able to outlast flood events for a certain time in the floodplain (Siepe 1989; Rothenbücher & Schaefer 2006). In contrast, ground beetle larvae are rather intolerant to hydrological stress (Den-Boer & Den-Boer-Daanje 1990) and therefore many species develop in less flood-exposed habitats (Rothenbücher & Schaefer 2006). Spring reproduction ensures reproductive success in these highly dynamic floodplain habitats, because early reproduction enables the larvae to develop in periods of low hydrological stress, thus increasing reproductive success (Thiele 1977). This also indicates that the survival strategies of ground beetles may be strictly geared to normal spring floods and that extreme summer floods have the potential to strongly affect community functioning. However, extreme event effects are rarely studied for ground beetles and it is still unknown whether the life-strategies of the species also fit extreme conditions, how resilient the communities are, and what impact extreme floods have on the functioning of ground beetle communities in floodplains.

# Purpose and structure of the dissertation

With this dissertation I aim to contribute to the research on the biodiversity effects of extreme environmental events. The main objective of this thesis is to better understand how ground beetles recover from unpredictable severe floods, and which ecological mechanisms exist to ensure the re-establishment of community functioning. In doing so, this work follows a synthesizing approach. First, the effects of an extreme flood event on ground beetle diversity will be analyzed and the taxonomical resilience estimated. This will serve as a basis for the core theme of the thesis, which is to identify the functional relationships between species and their environment and to evaluate how effective these relationships are when unpredictable weather extremes occur.

The thesis is composed of six chapters. In *chapter one* I will give a general introduction to the research field, outline the major aims of the study and present the general methodology applied.

*Chapter two* describes the taxonomical effects of the extreme Elbe flood on ground beetle communities. Based on a beta-diversity approach, this work shows (1) how quickly ground beetles recovered in terms of species richness and diversity, and (2) how long this recovery lagged behind the extreme flood. Whether communities which are differentially exposed to flooding, and therefore expected to be differentially adapted to flood disturbance, recovered faster than those rarely disturbed by flooding was also tested.

The following two chapters are important mediating parts for the fifth chapter of the thesis.

In *chapter three* a traits-based approach was used to identify the relationships between the environmental variability in floodplain grasslands and the functional characteristics of ground beetle communities. The chapter aims in a better understanding of ground beetle survival strategies under non-extreme environmental conditions. Therefore, it sets the basis to estimate if the strategies revealed here are also effective when ground beetles face extreme environmental disturbances.

In *chapter four*, a recently developed framework – functional diversity – was applied for the first time to ground beetle communities in fluctuating environments. Here it was analyzed how different aspects of functional diversity changed along a gradient of flood disturbance. The main objective was to test whether functional and species diversity react similarly to flood disturbance, and how species diversity governs functional diversity.

The main aim of *chapter five* was to identify the role of functional redundancy in maintaining ground beetle functioning after extreme floods. Functional redundancy means that some species perform similar roles for ecological processes, and that they can compensate for the loss of others and therefore promote ecological stability. Here I tested whether functional redundancy exists in floodplain ground beetles and whether it can buffer their functional diversity against extreme floods and therefore lead to high functional resilience.

*Chapter six* is a unifying chapter and combines the results and knowledge gained from the previous chapters: it compares taxonomic resilience to functional resilience, evaluates processes and survival strategies that are important under normal conditions, and discusses if these are appropriate also after extreme events. It finally serves to answer the initial research question: Can taxonomic and functional complexity buffer communities against extreme disturbances?

# The study area

The study was conducted in the floodplains of the Elbe River in the federal state of Saxony-Anhalt, Germany. With a length of 1,094 km and a catchment area of about 150,000 km<sup>2</sup>, the Elbe is one of the largest rivers in Central Europe (Scholten *et al.* 2005). The river has a pluvionivale flow regime with a higher discharge during winter and spring and low discharge from July to October. The mean annual discharge of the Elbe River ranges from 336 m<sup>3</sup>/s upstream to 730 m<sup>3</sup>/s downstream (Helms *et al.* 2002). Between the dams in the Czech Republic and the Geesthacht Weir near Hamburg, the river is not controlled by any barrages so that its flow regime is close to natural (Scholten *et al.* 2005). Nevertheless, a large proportion of the river banks are built up with dykes and groynes to allow shipping, and the inundation area of the river has been reduced by more than 80 % since the first half of the 19th century (IKSE 2001).

Fortunately, due to deficient maintenance and low degrees of technical development in the decades before 1990, many floodplain-typical structures have been preserved along the Elbe River and therefore its floodplains include large stretches of semi-natural areas and are ranked among the areas with the highest conservation value in Germany (Eichhorn, Rast & Reichhoff 2004). This is especially true for the coherent hardwood floodplain forests, which are among the largest coherent floodplain woodland complexes in Central Europe (Weiß & Peterson 2001). Besides floodplain forests, seasonally flooded grassland is one of the most common, but at the same time most endangered habitat types in the Middle Elbe region. It covers approximately 70 % of the total floodplain area and is mainly characterized by medium-intensity agricultural use (Scholz *et al.* 2005, Figure 2).



Figure 2 Typical habitat mosaic of the Middle Elbe region. Picture: Jürgen Roth, WWF.

Since 1979 the Elbe floodplains between Wittenberg and Magdeburg are internationally acknowledged as UNESCO Biosphere Reserve Middle Elbe. During the years after the political change in Germany, it was developed to a state-crossing Biosphere Reserve "Elbe Riverscape" with a length of more than 400 km (Puhlmann *et al.* 2009). With about 126,000 ha, the Middle Elbe Biosphere Reserve makes up the largest part of it. Besides a strong societal mission, it focusses on revitalizing morphological structures of the river and ecological processes in the floodplains.

Due to the near natural hydrologic regime of the Elbe River and its floodplains, the Middle Elbe region was an optimal choice for the purpose of this study. It is an area of high environmental variability caused by periodic alternations of flooding and droughts. As a consequence, this landscape is not only a refuge for highly specialized and threatened species, but also a place of complex interactions and relationships between species and their environment, the revelation of which was the prime aim of this dissertation.

# Study sites and data sampling

All research questions tackled by this thesis are underpinned by empirical data collected in the field. Here I will outline the general methodological approach to collecting the data, which is consistent throughout all chapters of the dissertation. Any deviations in data use or manipulation will be explained separately in each chapter.

The data used here originate from the projects RIVA and HABEX, which serve as a scientific and a methodological basis for this dissertation. A main requirement for both projects was that data should be collected in a highly standardized way. This was realized by applying a stratified randomized sampling design and proper documentation of environmental and species data (Henle *et al.* 2006).

In the course of RIVA, three study sites where established exclusively on seasonally flooded grassland, because of its representative status for the Biosphere Reserve Middle Elbe (Scholz *et al.* 2005). The main study site, "Steckby", is located near the village of Steckby (Elbe km 283–285), and the secondary sites near Wörlitz (km 242–243) and Sandau (km 417–418) respectively (Figure 3). In his dissertation, Böhnke (2001) gives a very detailed description of the hydrology, hydrogeological and geomorphological conditions of the study sites.



Figure 3 Study area and situation of the study sites in Germany, Artwork by Wilfrid Roloff, Berlin

All study sites were characterized by typical small-scale relief features, such as permanently and temporarily water-filled flood channels and elevated areas with lower flooding frequency and a low groundwater level. The more elevated and dryer areas were mown twice a year, whereas the wettest ones were usually not utilized. Each of the three study sites was grouped into three habitat strata on the basis of vegetation type and site morphology. The strata represent different habitat types, which are characterized by specific hydrological conditions (see Table 1 in Chapter two). The most elevated areas are characterized by a high groundwater depth and short inundation periods (habitat strata: fresh-dry grasslands). They are characterized by species assemblages belonging to the Dauco carotae-Arrhenatherum elatioris. Here, especially Galium verum, Agrostis capillaris, and Allium vineale indicate the low degrees of flood disturbance and the dry conditions. On the opposing gradient end, habitats located in floodchannels and depressions with high water permanency (habitat strata: wet grasslands) are characterized by species of the Ranuculetum aquatilis group with Lycopus europaeus, Rorippa amphibia and Xanthium albinum as abundant species, which can tolerate the anoxic conditions typically for these habitats. Species of Phalaraidetum arundinacae assemblages frequently occur in habitats close to permanent water bodies, for example Phalaris arundinacea and Iris pseudacorus. Largest in area is the mesophilous grassland type of Galio molluginis-Alopecuretum pratensis (habitat strata: moist grasslands), which is located in between the lowest (frequently flooded & wet habitats) and highest (rarely flooded and relatively dry habitats) areas. Here, *Elymus* repens can build up dominance stands in in the transition to floodchannel habitats, whereas Alopecu*rus pratensis* and *Arrhenatherum elatius* are most characteristic species of the higher situated areas.

The same number of sampling plots was placed randomly in each habitat strata, making up a total of 36 sampling plots on our main study site "Steckby" and 12 sampling plots each in "Wörlitz" and "Sandau" (see Figure 2 in Chapter two for a schematic design). On each sampling plot, five pitfall traps at a distance of five meters were filled with a 7% solution of acetic acid and a detergent to reduce surface tension. The traps were exposed for two 14-day periods from April to June and again for the same length of time from September to October 1998–1999, and again from 2002 to 2006, which resulted in an average trap exposure time of 30 days per sampling period. In the flood year 2002, all sampling sites were inundated for more than two weeks at heights from 1.60 m to 4.40 m. Sampling was carried out as soon as the floodwater receded but due to the long flood duration, the sampling period had to be adjusted backwards by a few days. All adults were identified by Arno Schanowski to the species level and stored in a solution of two-thirds ethanol (70% solution) and one-third acetic acid (60% solution). For each species, relevant biological traits were collected from standard identification keys and ground beetle compendia and stored in a database. I will explain in detail which traits were used for the specific research question in the respective chapters. See Henle *et al.* (2006) for a more detailed description of the study design.

The environmental characteristics of the sampling plots were intensively studied within the RIVA-project. On each plot, more than 300 environmental variables were recorded or derived from recorded data, ranging from hydrological to soil physical and chemical properties. In close collaboration with experts, Rink (2003) excluded highly correlated variables and filtered out the most important ones for each taxonomic group. For ground beetles in floodplains, hydrological variability emerged as one of the main drivers of species occurrence (Gerisch et al. 2006). Specifically, mean ground water depth and duration of inundation were the most important hydrological variables used in this thesis to relate with ground beetle occurrence. In the years 1998 and 1999, gauges for ground water (dipwell gauges) and water level (crest gauges) were installed on each sampling plot to measure maximum groundwater depth (in m), mean groundwater depth (in m), duration of inundation (in weeks) and inundation height (in m). Due to the high effort in cost and time required to continuously survey environmental variables, Follner & Henle (2006) developed a hydrological model that enabled them to obtain hydrological data without field measurements. For this, the plot-wise measurements from 1998 to 1999 were correlated with daily water level data of the Elbe River near to our study sites. By additionally accounting for evapotranspiration, the model calculated the selected hydrological variables for each plot and each sampling year after 1999. Throughout this work, I used the measured values of the hydrological variables for the years 1998-1999 and the values of the variables derived from the hydrological model for the post-flood years 2002–2006. Besides hydrological, also soil data and here especially sand content is important environmental driver for ground beetles. All soil measurements were taken in the years 1998 and 1999. More detailed information on the environmental variables used is found in the respective chapters.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

# CHAPTER TWO Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

# Abstract

Extreme environmental events are predicted to increase in future due to global climate change. However, their effects on biodiversity still remain insufficiently understood because of the rarity and consequently the difficulty of studying the effects of extreme events. Here, we investigate the impacts on ground beetles of an unpredictable catastrophic flood event of the Elbe River in Germany in the year 2002 using pre- and post-flood data. We analyzed the response of grassland communities differentially exposed to flooding and focused on the guestion of how long their response lagged behind this extreme flood. Ground beetles were sampled from 1998 to 1999 (pre-flood period) and from 2002 to 2006 (post-flood period) on 48 floodplain grassland plots with a stratified randomized sampling design. Community resilience was guantified by calculating changes in species richness, species abundances, Simpson diversity and beta diversity of ground beetle assemblages. Ground beetles showed low resistance but high resilience to the extreme flood. Species richness decreased strongly immediately after the flood but reached pre-flood values 2 years later. However, beta diversity remained relatively high in the subsequent years indicating persistent shifts in species composition and abundances. Contrary to our expectation, assemblages inhabiting plots prone to flooding, expected to be less sensitive to floods, did not recover faster than those on rarely inundated plots. We considered both the timing and the long duration of the flood as main reasons for the low community resistance to the flood. Strategies related to dispersal and habitat generality are identified to be crucial for the quick community recovery following the extreme flood. Our results endorse that extreme floods are integral parts of functioning floodplain ecosystems and that species can cope well even with such unpredictable extreme events, although recovery time tends to be longer than after normal floods.

**Keywords:** Carabids, community succession, invertebrates, recolonization, stability, stochastic disturbance, streams, survival strategies

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Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

# Introduction

A major paradigm in ecology is that environmental perturbations mould the structure and function of biological systems (Tilman & Downing 1994; Lake 2000). To maintain ecological integrity after disturbances, resilience is a crucial feature for floral and faunal communities (Elmqvist *et al.* 2003). Resilience is the capacity of habitats, communities or species to return to a prior state following a disturbance (Grimm & Wissel 1997; Gunderson 2000) and can therefore be defined as the return time for biological systems to recover to their initial state (Ives 1995). Over recent years, a great deal of effort has been put into investigating how long the response of biodiversity lags behind disturbance events, i.e. how long the effects of disturbances are visible in communities (e.g. Collier & Quinn 2003; Hancock 2006; Moretti, Duelli & Obrist 2006; Ballinger, Lake & Nally 2007). One major outcome from these studies is that resilience can differ considerably among and within taxonomical groups and that resilience depends strongly on the life-history strategies as well as behavioural and morphological adaptations of species (Lytle, Bogan & Finn 2008; Ilg *et al.* 2008a).

Most of this knowledge about disturbance and resilience is derived from numerous studies of relatively regularly occurring disturbances of limited magnitude. In contrast, our understanding of the effects of extreme and unpredictable environmental events on ecosystem stability is still rudimentary (Jentsch et al. 2009), even in highly variable systems. However, the capacity of communities to recover from disturbances is of particular importance in highly dynamic ecosystems, such as floodplains (Tockner et al. 2002). In the temperate zones, floods occur episodically, with high discharge in spring due to snowmelt in the upstream mountains and increased precipitation, whereas discharge is low during the summer season. Floodplain species must possess special strategies to cope with these regular disturbances (Robinson, Tockner & Ward 2002). Weigmann & Reiche (1999) pointed out that most terrestrial invertebrates in Central European floodplains are opportunistic habitat generalists with high reproduction rates and high dispersal power, being crucial traits for repeated recolonization of intermittently flooded areas. Furthermore, both adults and larvae of many species are flood resistant, but adult species additionally can show specific behavioural predispositions to flooding, such as vertical migration or preying under water (Adis & Junk 2002). Due to the seasonality of floods in temperate zones, many riparian invertebrates develop during the drier summer season to minimize the risk of larval mortality during winter floods (Robinson et al. 2002).

Regularity and temporal and spatial shifts of environmental conditions are the main drivers for species assemblages predisposed to floodplain dynamics and lead to the high biodiversity of riparian habitats (Henle *et al.* 2006). With ongoing climate change, floodplains are predicted to be faced increasingly with catastrophic floods and long-lasting droughts, occurring beyond the regularity that is typical for the temperate zone (Whited *et al.* 2007; Borken & Matzner 2009). As for other extreme events, the effects of extreme floods on species, communities and biodiversity dynamics were rarely quantified in the past and are thus poorly understood. For plants, Vervuren, Blom & de Kroon (2003) stressed that extreme events can determine the distribution and occurrence of species for many subsequent years. Hering *et al.* (2004) could not reveal significant impacts of an extreme flood on vegetation and benthic invertebrates, but did reveal a very strong response of riparian ground beetles. For molluscs, Ilg *et al.* (2008b) showed that an extreme flood favoured the colonization of aquatic species and Plum & Filser (2005) noted that annelid populations were strongly reduced by an extreme flood. One major outcome of these

CHAPTER TWO 22 Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

studies is that unpredictable extreme floods can cause catastrophic declines in both biomass and species richness (Ballinger *et al.* 2007; Thibault & Brown 2008) and lead to severe changes in community structure and composition (Parsons *et al.* 2005; Strausz & Janauer 2007), which can persist for many years after the event (IIg *et al.* 2008a).

Several studies report on the effects of regular and periodic flooding on biodiversity, including ground beetles as one of the most species rich and abundant macroinvertebrate taxon in semiterrestrial habitats (e.g. Greenwood et al. 1995; Bell et al. 1999; Antvogel & Bonn 2001; Framenau, Manderbach & Baehr 2002; Bonn et al. 2002; Sadler et al. 2004; Rothenbücher & Schaefer 2006; Looy et al. 2007; Lambeets et al. 2008). Overall, these studies outline that riparian ground beetles are highly resilient to regular, periodic floods, as most of these species use a "risk strategy", combining high reproduction, dispersal and remigration rates following disturbances (Zulka 1994; Adis & Junk 2002). Lambeets et al. (2008) showed that flight ability, i.e. high mobility, is a major advantage of floodplain ground beetles to cope with increasing flood disturbance. Studies of Thiele (1977) and Den-Boer & Den-Boer-Daanie (1990) assumed that the activity peak during the low water periods in late spring and summer is crucial for a successful reproduction and minimizes the environmental stress for the larvae that generally develop during the summer. This suggests that the resilience of ground beetles of temperate floodplains is closely connected to floods occurring in winter or spring. Consequently, one may assume that unpredictable and extremely intense summer floods have the potential to strongly affect ground beetle communities because species pre-dispositions to flooding may be strictly geared to a specific disturbance season (Lytle & Poff 2004).

In a preliminary study, Ilg *et al.* (2008a) compared the response of three different taxonomical groups to a catastrophic flood and found the strongest response in ground beetle communities. Here, we present an in-depth study using an extended dataset to quantify community resilience of ground beetles to this extreme flood event. Our aims were to determine (i) how long ground beetle assemblages took to recover from the extreme flood, and (ii) whether species communities inhabiting habitats that are differentially exposed to floods differ in their resilience in terms of species richness, abundance and species composition. We hypothesized a quick community recovery due to the high dispersal and recolonization power of alluvial ground beetles. Furthermore, we assumed that communities of flood prone habitats showed a quicker recover than communities of less frequently inundated areas.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

# **Material and Methods**

#### Study area

The Elbe River is the third largest stream in Germany and ranks among the largest rivers in Europe. It flows from the Giant Mountains in the Czech Republic to the North Sea near Cuxhaven (Germany), after covering a distance of about 1,100 km and draining a catchment of about 150,000 km<sup>2</sup>. The mean annual discharge of the Elbe River ranges from 336m3/s upstream to 730m3/s down-stream. The water level is mainly dominated by snowmelt in spring and erratic precipitation over the year, inducing high discharge in winter and spring, and low discharge in summer (Scholten et al., 2005). From the German-Czech borders to the weir in Geesthacht near Hamburg, the stream's hydrology is not affected by barrages and the flow regime is thus considered natural. However, a large proportion of the river banks are built-up with dykes and groynes to allow shipping.

Our study was conducted in the course of the RIVA project (Dziock et al. 2006) at two study sites "Steckby" and "Wörlitz", located close to the city of Dessau in Saxony Anhalt, Central Germany, and within the UNESCO Biosphere Reserve "Elbe River Landscape" (Figure 1). This area is characterized by landscape mosaics of native floodplain forests and extensively managed floodplain grasslands. For our study, we selected seasonally flooded grassland with typical small-scale relief features, such as temporary water-filled flood ditches and elevated areas with lower flooding frequency and low groundwater level. The elevated areas were mown twice a year, whereas the lower, water-filled depressions were excluded from utilisation.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream



**Figure 1** Position of the study sites within the Elbe catchment (A) and position of the sampling plots in the stratified random sampling scheme within the main study site 'Steckby' (B). This figure is available in color online at wileyonlinelibrary.com/journal/rra.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

In the summer of 2002, unpredictable severe precipitation led to the highest flooding ever recorded along the River Elbe. Some even regard it as one of Europe's biggest natural disasters in living memory (Schiermeier, 2003; Petrow et al. 2007). This flood was extreme in terms of its height, duration, and seasonal and spatial occurrence (Figure 2).



**Figure 2** Hydrograph of the Elbe River at gauge station Aken/Elbe. Data are expressed as daily river gauge values for each year. For clarity the figure is divided: (A) shows the data before the catastrophic flood and a 10-year average (1991–2000); (B) shows the data for the catastrophic summer flood (2002) and all subsequent sampling years. Data source: Waterways and Shipping Office Dresden, Germany. This figure is available in color online at wileyonlinelibrary.com/journal/rra.

# Ground beetle sampling and hydrological variables

Sampling was carried out on 36 plots located on the study site "Steckby" and 12 plots located on the study site "Wörlitz". The plots were chosen following a stratified randomized design. The study sites were grouped into three habitat types regarding vegetation and obvious humidity conditions. The position of the sampling plots was randomized within each of the three habitats (Figure 1B; see Henle et al. (2006) for a detailed description of the study design). On each plot, five pitfall traps were installed and filled with a 7 % solution of acetic acid and a detergent to reduce surface tension. A differential GPS "Trimble 5700" was used to place the traps on exactly the same location in each sampling year.

The traps were retrieved bi-weekly from September to October in the years 1998 – 1999 and from 2002 to 2006. Sampling in the flood year 2002 was carried out as soon as the floodwater receded. Due to the long flood duration in 2002, the sampling period had to be adjusted backwards for a few days. We had an average trap exposure time of 30 days per sampling period.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

The samples were sorted out and stored in a mixture of one-third acetic acid (60 % solution) and two-thirds ethyl alcohol (80 % solution). All adult ground beetles were identified to the species level.

In the years 1998 and 1999, gauges for ground water (dipwell gauges) and water level (crest gauges) were installed on each sampling plot to measure maximum groundwater depth (in m), mean groundwater depth (in m), duration of inundation (in weeks) and inundation height (in m). Due to the high effort in cost and time to continuously survey environmental variables, Follner and Henle (2006) developed a hydrological model that enabled us to obtain hydrological data without field measurements. For this, the plot-wise measurements from 1998 to 1999 were correlated with daily water level data of the Elbe River near to our study sites. By additionally accounting for evapotranspiration, the model calculated the selected hydrological variables for each plot and each sampling year after 1999. Our analysis used the measured values of the hydrological variables for the years 1998 – 1999 and the values of the variables derived from the hydrological model for the post-flood years 2002 – 2006.

#### Data manipulation and analysis

Altogether, we lost 17.5 % of our pitfall traps (n = 588) during the whole study period due to water-level fluctuations and the destruction through wild boars. To account for the loss and also for the slight differences in the length of our sampling periods, we standardized the ground beetle abundances by the number of functioning trap-days, to obtain comparable data among the sampling years:

$$ns_{ij} = \frac{n_{ij}}{(t_j d_j)}$$

with  $ns_{ij}$  the standardized individual numbers of species i on sampling plot j,  $n_{ij}$  the total number of recorded individuals of species i on plot j,  $t_j$  the number of traps functioning at sampling plot j, and  $d_j$  the number of sampling days on plot j. We used the standardized abundances for all subsequent statistical analyses.

A non-hierarchical cluster analysis "Partitioning Around Medoids" (PAM) was applied to our hydrological variables to group the sampling plots according to groundwater level and flood duration, being important environmental variables for floodplain ground beetles (Gerisch *et al.* 2006). The use of PAM instead of hierarchical cluster methods is recommended by (Van der Laan, Pollard & Bryan 2003) due to the possibility of flexible cluster definition and the insensitivity to outliers. Another advantage is that the numbers of clusters selected can be verified with the criterion of average silhouette width, which in our case was highest (asi = 0.49) at a construction of three groups. A linear discriminant analysis and permutation tests (9,999 iterations) showed a high significance of the cluster separation (p < 0.001). For the analysis, all variables were standardized to a zero mean and unit variance prior to the analysis. The clusters of plots with different hydrological conditions (Table 1), which are referred to as humidity classes in the following, correspond well to certain habitat types: humid grassland inundated for relatively long periods (humidity class I), intermediate grasslands with medium flood duration (humidity class II), and elevated and drier meadows with short inundation periods (humidity class III).

# Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

Humidity class	Inundation		Groundwater depth		Habitat		
	Height (m) ± MAD	Duration (weeks) ± MAD	Maximum (m) ± MAD	Mean (m) ± MAD			
I (n = 20)	2.03 ± 1.05	20 ± 10.38	-1.59 ± 0.53	-0.39 ± 0.47	humid grassland/ flood ditches		
II (n = 14)	1.29 ± 0.69	4 ± 4.45	-2.90 ± 0.56	-1.52 ± 0.76	intermediate grasslands		
III (n = 14)	0.51 ± 0.76	1 ± 1.48	-3.88 ± 0.34	-2.78 ± 0.50	elevated, drier meadows		

**Table 1** Hydrological classification of the sampling plots, revealed by Partitioning Around Medoids. Data expressed as median among the sampling years and median absolute deviation (MAD).

In a another study, we tested for spatial autocorrelation of species richness and diversity by means of Moran's I and found only little spatial dependence of those metrics (Gerisch 2011). Therefore we decided to neglect the effects of spatial autocorrelation in this study. Correspondence discriminant analysis (CDA) was used to identify the flood impacts on ground beetle communities. CDA is an extension of the correspondence analysis proposed by to compare variables (standardized abundances) belonging to several groups (sampling years). The standardized abundance dataset was log-transformed to increase the homoscedasticity and normality of our data. Permutation tests with 9,999 iterations were used to verify the statistical significance of the between-group discrimination.

We considered the changes in species richness, standardized abundances, Simpson diversity, and beta diversity as measures of ground beetle community resilience to the extreme flood event. Simpson diversity combines species richness, species abundances and additionally the evenness of abundances into a measure of diversity and thus should be able to reveal different aspects of community resilience. We used the Morisita-Horn index as a measure of beta diversity to calculate the community change of a plot between a particular sampling year and a reference year. This quantitative index is based on species composition and abundance and its use is recommended by Taylor (1986) and Krebs (1999) because of its robustness. It ranges from 0, indicating identical taxa composition, to 1, indicating total community turnover of a plot between the compared years. We chose 1999 as a reference year for species composition and species abundances, as the year 1998 lacked a typical spring flood and was remarkably drier than 1999 (see also Figure 1A in Chapter one). The statistical significance of the shifts of the measures was tested with a pairwise Wilcoxon rank sum test with Benjamini & Hochberg correction to adjust p-values. All multivariate analyses were conducted with the GPL software R (R Development Core Team 2010) and the packages vegan, ade4, and cluster.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

# Results

#### Flood impacts on ground beetle communities

Our dataset consisted of a total of 42,045 individuals representing 128 species. For a full species list including pre- and post flood abundance data, information on flight ability, reproduction strategy, and humidity preference, see Supplementary Material 1. Both ground beetle species richness and abundances were strongly affected by the 2002 summer flood. Compared to 1999, we sampled less than 50 % of the species and only 20 % of the individuals immediately following the flood in 2002 (Table 2). However, the abundances of a few species remained stable or even increased. For example, the total abundance of *Trechus quadristriatus* increased from 113 in 1999 to 1,192 individuals directly after the flood, which accounts for 82 % of all trapped individuals in 2002.

**Table 2** Ground beetle species richness and individual numbers among the sampling years. Asterisksindicate a significant change to the reference year 1999 (Wilcoxon test, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001).MAD = median absolute deviation.

Sampling year	Total number of recorded species	Median number of species/plot ± MAD	Total number of recorded individuals	Median number of individuals/ plot ± MAD	Median indi- vidual num- ber/trap day/plot ± MAD
1998	80	18.5 ± 7.4	8,776	150.0 ± 113.4	0.87 ± 0.38
1999	79	15.0 ± 5.9	7,581	154.5 ± 106.8	0.80 ± 0.39
2002	37	3.0 ± 1.5***	1,453	21.0 ± 20.8**	0.20 ± 0.13***
2003	64	11.0 ± 4.5***	2,867	41.0 ± 28.9**	0.30 ± 0.16***
2004	70	16.0 ± 4.5	6,401	116.5 ± 81.1	0.63 ± 0.34*
2005	73	15.5 ± 5.2	6,038	123.5 ± 77.1	0.67 ± 0.28*
2006	76	14.5 ± 5.9	8,929	143.0 ± 91.9	0.73 ± 0.37

The first two axes of the correspondence discriminant analysis explained 39.4 % of the total variance (Figure 3). A permutation test revealed statistical significance of the discrimination (p < 0.01). The distinct position of the year 2002 is mainly caused by the disappearance of approximately 50 % of the pre-flood species and the massive abundance decrease of most remaining species. In contrast, *Trechus quadristriatus* and *Loricera pilicornis* showed an abundance increase and thus contributed most to the exposed position of the 2002 communities in the ordination plot. *Agonum dolens* was recorded only in the flood year, most likely caused by drifting from upstream areas. Figure 3 shows that the pre-flood communities were strongly characterized by the hygrophilic species *Bembidion gilvipes* and *Epaphius secalis*, which occurred in high abundances both in flood ditches and on elevated areas. However, the abundances of both species declined dramatically after the flood. Ubiquitous species like *Carabus granulatus*, *Nebria brevicollis* and *Poecilus cupreus* strongly increased in abundance following the extreme flood.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

However, we also recorded typical alluvial species like *Oodes helopioides*, *Bembidion dentellum* and *Anisodactylus binotatus* in very high abundances compared to the pre-flood period (see Supplementary Material 1).



**Figure 3** Ordination of the sampling plots according to a CDA of the species-plot dataset separated by sampling years. Points refer to the sampling plots. Superimposed species contributed most to the discrimination of the sampling years. Labels of species and sampling years are placed at their centroid position. Ellipses represent the summarized weighted scatterplot for each sampling year.

# Recovery of species richness, species abundance, and species composition

Total species richness increased quickly to a level similar to that of pre-flood conditions within two years of the extreme flood (Table 2). Although species richness was very low on all plots immediately after the flood in 2002, communities inhabiting frequently inundated plots (humidity class I) were most affected by the extreme flood, losing 84% of their species and up to 90% of their individuals. We could not identify significant differences in the recovery of species richness

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

of the different humidity classes. There was, however, a trend that species numbers recovered faster on the elevated, dry plots (humidity class III) and that those habitats slightly exceed the pre-flood values (Figure 4A, see Supplementary Material 2 for significance tables).



**Figure 4** Ground beetle species richness (A) and standardized relative abundances (B) among sampling years and among humidity classes. Box plots are shown with median, 25 and 75 %-quartiles, and max/min values. Single outliers marked as dots. See Table 1 for cluster description and Supplementary Material 2 for significances.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

Similar to total species richness, overall species abundances increased quickly and had already reached pre-flood levels two years after the extreme flood (Table 2). Compared to the more flood exposed plots, the flood-response of communities inhabiting exposed, dry plots was less pronounced (Figure 4B). We identified a similar trend as for species richness, although not statistically significant, that abundances of the more elevated plots recovered faster and exceeded the original pre-flood values. In contrast, species abundance recovery of the humid plots was not finished until 2006 (p < 0.05, Wilcoxon test, see Supplementary Material 2).

Ten species were not re-recorded after the extreme flood in 2002, but we trapped 28 new species, although most of them with only a few individuals. Three species, *Trechus quadristriatus*, *Nebria brevicollis* and *Loricera pilicornis* showed a comparable strong abundance increase immediately after the flood in 2002 but decreased again towards pre-flood levels in the subsequent years. Relative abundances of *Pterostichus melanarius*, *Anisodactylus binotatus* and *Bembidion dentellum* were considerable higher during the post-flood period compared to the years prior to the flood. However, the majority of the species showed a rapid recovery from the abundance declines (see Supplementary Material 1).

The extreme flood considerably affected also the Simpson diversity of ground beetles. In general, the diversity measure showed similar temporal patterns like species richness and abundances: a strong decline in 2002 and a rapid increase towards pre-flood values in the subsequent years (Figure 5A and Supplementary Material 2). Moreover, it also indicates that the evenness of species abundances were seriously affected, due to single abundant species, but quickly recovered following the flood.

The observed shifts in species composition, abundance, and diversity in the flood year 2002 caused beta diversity rates close to the maximum possible in all three humidity classes (Figure 5B). Community change decreased in 2003, indicating that community composition and abundance structure approached pre-flood conditions. However, beta diversity decreased only slightly in the following years, except for the elevated plots. The dissimilarity at the end of our study period was highest for communities inhabiting the flood ditches and much lower for communities inhabiting the drier, elevated plots. Even in 2006, i.e. four years after the flood, communities inhabiting flood exposed plots differed by up to 40 % from species composition of the reference year 1999. In contrast, community changes in the elevated plots were not significantly different to pre-flood conditions within two years of the flood (Supplementary Material 2).

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream



**Figure 5** Changes in Simpson diversity (A) and beta diversity (B) of ground beetle communities of the different humidity classes based on the reference year 1999. Beta diversity was calculated as the Morisita–Horn index. A value of 1 indicates complete dissimilarity, a value of 0 indicates complete similarity. Outliers are marked as dots. Box plots are shown with median, 25 and 75 %-quartiles, and max/min values. Single outliers marked as dots. For significance tables, see Supplementary Material 2.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

### Discussion

Dispersal power and habitat generality facilitated community recovery

In this study we found ground beetle community resistance to an extreme summer flood to be very low, as shown by the community turnover rates close to the maximum possible immediately after the flood. This low community resistance, i.e. the strong decrease in species numbers and abundances following the flood, is in line with most of the studies dealing with catastrophic floods and terrestrial invertebrates. Hering *et al.* (2004) recorded the lowest densities of ground beetles one month after an extreme flood in an alpine floodplain. A similar pattern was also detected by Ballinger *et al.* (2007) for species richness and abundance of ants after a major flood in an Australian floodplain. In contrast, species groups being highly dependent on water saturated conditions, such as molluscs or chironomids, can increase in species richness and abundances after extreme flooding (Palmer *et al.* 1995; Ilg *et al.* 2008b). These differential responses indicate that community resistance to flood disturbance mainly depends on the life-strategies and the ecological requirements of the species (Robinson *et al.* 2002; Ilg *et al.* 2008a).

On an intermediate time scale, however, ground beetle communities possessed high resilience, as species numbers, abundances and Simpson diversity quickly increased towards pre-flood levels. Recent studies assume dispersal power and reproductive traits as especially responsible for the high recovery rates of ground beetles after flooding (Bates, Sadler & Fowles 2006; Lambeets et al. 2008). In this study, we identified a combination of habitat generalism and high dispersal power that enabled ground beetle communities to quickly recover from the extreme flood. On a short time scale, i.e. immediately following the flood in 2002, species with low habitat requirements were most abundant. This is in line with Adis & Junk (2002), stating that large numbers of floodplain invertebrates are habitat generalists being able to quickly recolonize disturbed plots. In our study, this was especially true for the very ubiquitous species Trechus quadristriatus, Nebria brevicollis and Pterostichus melanarius which were the most abundant species immediately following the flood. These species quickly colonized the drying plots from the surrounding elevated woodland habitats. In contrast, most refuge habitats of truly alluvial species were still flooded. Among habitat generality, high dispersal power is often regarded as crucial for the survival of ground beetles under changing environmental conditions and for rapid habitat recolonisation after disturbances (Ribera et al. 2001; Pizzolotto 2009). Our results also support this, as most of the good dispersing species were already present again one year after the flood and several of them reached pre-flood abundance levels two years later. Reproductive traits may also have influenced ground beetle recovery to the extreme flood. Some species, e.g. Bembidion gilvipes, Amara bifrons, Calathus melanocephalus or Epaphius secalis showed considerable and persistent abundance declines in the post-flood years. We assume that the flood timing coincided with the larval development of these species leading to a reproduction breakdown following the flood. Hering et al. (2004) also reported on increased larval mortality of ground beetles following an extreme flood. Therefore, another important strategy determining community resilience was most likely being adult at the particular flood time, which enabled the organisms to actively evade the flood by flying, swimming or hiding in refuges, minimizing the hydrological stress for the larvae. Nevertheless, comparatively little is known about the biology of the ground beetle larvae, and the reproduction effects of environmental variability.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

#### Highest beta diversity of plots experiencing frequent inundation

Our results confirm the findings of Barrat-Segretain & Amoros (1996) and Ballinger *et al.* (2007) in terms of plots prone to flooding being the most affected ones after major floods. In contrast to their results, however, we found no evidence that communities particularly exposed to floods recovered faster than the ones inhabiting elevated areas. Rather, we observed the opposite: communities recovered quicker on the drier and more elevated plots. These opposing observations may be explained by a long lasting winter flood in our case that prevented the recolonisation of lower flood ditches for a considerable time period. Since the floodwaters receded much earlier from the elevated plots, the rate of community recovery was rather a function of the time after drying than a matter of the habitat type.

The time lag in recolonisation of the flood ditches probably was additionally affected by an extremely hot and dry summer in 2003 (Schär & Jendritzky 2004). In that year, the flood ditches dried out completely for an unusually long time period. Consequently, the dried habitats were colonized by ubiquitous species, such as *Nebria brevicollis* or *Poecilus cupreus* and xerophilous species, such as Amara equestris or Calathus fuscipes. Similar effects were noted for floodplain molluscs in France, which were severely affected by that summer drought (Mouthon & Daufresne 2006). These shifts in community composition, as well as strong abundance shifts of single species, e.g. T. quadristriatus, lead to the relatively high community turnover rates observed in this study. The most obvious example for the latter is *T. quadristriatus*, with a tenfold abundance increase immediately following the flood and a quick decrease one year later. Dominance shifts of species as well as the single dominance of species are frequently observed in disturbance related studies. For example, Moretti et al. (2006) reported on strong abundance shifts of invertebrate species following fire events, assuming relationships between certain functional traits and the competitive power of species. Niemelä & Kotze (2009) found few highly dominant carabid species on the most disturbed sites along an urbanization gradient and assumed habitat generality as the main reason for the observed patterns. Here we also explain the observed abundance shifts directly following the flood by the functional traits of habitat generalist species. With the total reset of the communities in 2002, habitat generalists could occupy free functional niches, e.g. related to food availability, also in habitats originally inhabited by alluvial species. With ongoing habitat succession, truly alluvial species also resettled the flood ditches but, contrary to our expectation, abundances of many generalists remained on relatively high levels. This shows that those species were also able to exploit similar resources as habitat specialists for a certain time-frame. However, we assume that other factors like geographical distribution, rarity, or the specificity to certain environmental conditions also play important roles for species recovery.

#### Methodological limitations in the study of extreme events

Analyzing the impacts of extreme events poses major methodological challenges. By their very nature, extreme events are generally singular events without spatial or temporal controls being available. Therefore, practically all our knowledge on the effects of extreme events on biodiversity depends on an evaluation of data collected in the same area before and after an extreme event – and these data rarely can be precisely standardized. We were fortunate to achieve a very high standardization due to the use of high resolution GPS, a detailed sampling design, and elaborate documentation of all data (Henle *et al.* 2006). Nevertheless, a discussion of the methodological limitations in the study of extreme events is warranted. The relatively restricted area of our study sites poses the question of spatial independence of our data.

Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream

We used a stratified random sampling design to reduce such effects and I found only very weak spatial autocorrelation of the data (Gerisch 2011). Restraining the sampling to a limited area has the advantage that an influence of the species pool of the surrounding landscape could be minimized. However, community dynamics after an extreme flood may differ in landscapes with species pools that differ in their trait composition from our study. The same might be the case in floodplain grassland with other management regimes. These possibilities can be assessed only when sufficient numbers of studies that took advantage of similar extreme events become available for a meta-analysis.

As there is no temporal control of the extreme flood event, one might argue that the changes observed by us might be due to other factors. However, no other factor showed any major change and it is well-known that hydrological conditions are a major driver of the dynamics of floodplain communities (Robinson *et al.* 2002; Ilg *et al.* 2008a). One might also argue that the particularly strong change from pre- to post-flood community structure may be due to the time accumulated as our last pre-flood data were collected three years before the extreme event occurred. The comparably modest differences between 1998 and 1999 as well as between 2003 and 2006 are incompatible with such an interpretation. Also, the unusually dry conditions of 2003 did not cause a similar deviation of community structure from the remaining years as did the extreme flood in 2002.

#### Conclusion and outlook

The most important result of this study is that the extreme flood in 2002 did not cause significant changes in ground beetle communities over a period of four years. We show that ground beetles were considerably resilient to an extreme summer flood, although being heavily affected immediately following the flood. This indicates that the survival strategies of alluvial ground beetles, e.g. high reproduction rate and high dispersal capacity, are successful strategies to cope with even extreme, aperiodic disturbances. We thus conclude that extreme floods, besides regular flooding, are integral parts of floodplain ecosystems and important drivers for the high diversity of these habitats. Moreover, the tabula-rasa effects of extreme floods can completely reset species composition and enable the succession of degraded communities, which is especially important in the case of regulated rivers. By creating new ecological niches, or "cleaning" existing ones, such disturbances are particularly responsible for the spatio-temporal cohesion of habitats along rivers and thus play important roles for metapopulation dynamics. However, there are still knowledge gaps regarding how such population dynamics, and thus the community resilience to extreme events, are controlled, or even dependent on the life-history traits of the species. Future work should therefore determine the mechanistic linkages between extreme events, life-history traits, and species response patterns and take advantage of extreme events whenever they occur, despite the considerable methodological challenges they pose.
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# Appendices

**Supplementary Material 1** 1/5 Ground beetles recorded during the study with additional information on the biology of the species. Abbrevations: flight = flight ability, repr = season of reproduction, hygr = humidity preference, mac = macropterous (winged), br = brachypterous (unwinged), dm = dimorph (winged and unwinged individuals), spr = spring, aut = autumn, h = hygrophilous, x = xerophilous, u = ubiquitous.

Species	Indiv	vidual	num	oers				Biolog	У	
	1998	1999	2002	2003	2004	2005	2006	flight	repr	hygr
Acupalpus exiguus	11	26		1	9	7	6	mac	spr	h
Acupalpus meridianus		1						mac	spr	h
Agonum dolens			5					mac	spr	h
Agonum duftschmidi		12		2	4	2	1	mac	spr	h
Agonum emarginatum	5	16	1	40	52	19	17	mac	spr	h
Agonum fuliginosum	17	16			8			dm	spr	h
Agonum lugens				1	1	2	3	mac	spr	h
Agonum marginatum				1			1	mac	spr	h
Agonum micans	2	2	6	3	8	1	6	mac	spr	h
Agonum piceum					1		2	mac	spr	h
Agonum thoreyi					1			mac	spr	h
Agonum versutum		1	9	3	1	1	8	mac	spr	h
Amara aenea		2					2	mac	spr	х
Amara apricaria		1			4			mac	aut	е
Amara aulica	9	13		1	7	45	257	mac	aut	е
Amara bifrons	30	30		5	5	4	4	mac	aut	х
Amara communis	84	101	1	8	71	50	35	mac	spr	е
Amara convexior	2	1		3				mac	spr/aut	х
Amara equestris	19	236	3	109	79	55	72	mac	aut	х
Amara eurynota					4		1	mac	spr/aut	х
Amara familiaris	2	2				5		mac	spr	е
Amara lunicollis	33	39		37	124	51	20	mac	spr	е
Amara majuscula	1	1		1				mac	aut	е
Amara municipalis			1					mac	aut	х
Amara ovata	1	3		2	12			mac	spr	Х
Amara plebeja	48	12		7	22	4	1	mac	spr	h
Amara similata	3	3		2	31	3		mac	spr	е
Amara strenua		5		7	7	5	23	mac	spr	h

Supprementary mate	1	2/5								
Species	Indiv	vidual	numl	oers				Biolog	У	
	1998	1999	2002	2003	2004	2005	2006	flight	repr	hygr
Amara tibialis		1				2		mac	spr	х
Anisodactylus binotatus	23	76		25	129	241	295	mac	spr	h
Anisodactylus signatus					2			mac	spr	h
Anthracus consputus		1		1	1	1	1	mac	spr	h
Badister bullatus	3	1		2	3		2	mac	spr	е
Badister collaris				1				mac	spr	h
Badister dilatatus	1	1						mac	spr	h
Badister lacertosus	1							mac	spr	h
Badister meridionalis						1	1	mac	spr	h
Badister unipustulatus	4	2	1	2	10	3	4	mac	spr	h
Bembidion assimile						9	3	dm	spr	h
Bembidion biguttatum	6	45		16	48	40	54	mac	spr	h
Bembidion dentellum	11	14	9	154	149	81	101	mac	spr	h
Bembidion fumigatum						2		mac	spr	h
Bembidion gilvipes	211	196			4	8	20	dm	spr	h
Bembidion guttula	11	23			20	12	50	dm	spr	h
Bembidion lampros	1		1			2		dm	spr	е
Bembidion lunulatum		1		2		1		mac	spr	h
Bembidion minimum							1	mac	spr	h
Bembidion obtusum	1		1					dm	spr	е
Bembidion properans	10	15	1		1			dm	spr	h
Bembidion quadrimaculatum	16	7	5	1	3	1	11	тас	spr	е
Bembidion quadripustulatum				1				mac	spr	h
Bembidion semipunctatum			1					mac	spr	h
Bembidion tetracolum		1	1	2	11	4	2	dm	spr	h
Bembidion varium	1							dm	spr	h
Blethisa multipunctata			1					mac	spr	h
Brachinus explodens		1						mac	spr	х
Bradycellus harpalinus	4	1			1	1	1	br	spr	х
Calathus fuscipes	32	77		6	112	113	74	dm	spr	Х

Supplementary Material 1 2/5

Supplementary Mate	rial 1	3/5									
Species	Indi	vidual	numl	oers				Biolog	Biology		
	1998	1999	2002	2003	2004	2005	2006	flight	repr	hygr	
Calathus melanocephalus	281	140	1	20	44	52	63	dm	aut	Х	
Calosoma auropunctatum							1	mac	spr	х	
Carabus auratus							1	br	spr	Х	
Carabus glabratus						11		br	spr/aut	h	
Carabus granulatus	58	86	1	16	187	427	92	br	spr	h	
Carabus hortensis		2						br	aut	е	
Carabus nemoralis	113	4	1		7	4	1	br	spr	h	
Carabus violaceus		3						br	aut	h	
Chlaenius nigricornis		2		1		1	1	mac	spr	h	
Clivina fossor	106	88	16	23	53	70	65	dm	spr	h	
Cychrus caraboides	4					1	1	dm	aut	h	
Demetrias atricapillus	1							mac	spr	е	
Demetrias monostigma	4	1			6		2	br	spr	h	
Diachromus germanus	1			1				mac	spr	h	
Dyschirius aeneus	1	1						mac	spr	h	
Dyschirius globosus	31	13	1		10	12	3	dm	spr	h	
Dyschirius luedersi					1			mac	spr	h	
Elaphropus parvulus			1					mac	spr	h	
Elaphrus riparius			1					br	aut	h	
Epaphius secalis	756	517			5	46	80	mac	spr	Х	
Harpalus affinis	1				3	1	3	mac	aut	Х	
Harpalus calceatus	1	1		1				mac	spr	е	
Harpalus distinguendus						2		mac	spr/aut	Х	
Harpalus froelichii				1	1			mac	spr/aut	х	
Harpalus latus	4	8	1	1	4	4	6	mac	spr/aut	h	
Harpalus luteicornis	1			3	4	1	8	mac	spr/aut	х	
Harpalus rubripes	1	1			1			mac	spr	х	
Harpalus rufipes	103	81	3	166	61	26	99	mac	aut	е	
Leistus ferrugineus	23	9						dm	aut	х	
Leistus terminatus	16	3					2	dm	aut	h	
Limodromus assimilis				9	2	3	1	br	spr	h	

Supplementary Mater	rial 1	4/5								
Species	Indiv	vidual	numł	oers				Biolog	У	
	1998	1999	2002	2003	2004	2005	2006	flight	repr	hygr
Loricera pilicornis	5	4	37	16		12	8	mac	spr	h
Masoreus wetterhallii							1	dm	aut	Х
Microlestes minutulus	3	12		7	12	1	5	mac	spr	Х
Nebria brevicollis	18	6	56	580	2065	1035	17	mac	aut	h
Notiophilus aesthuans			1					mac	spr/aut	Х
Notiophilus aquaticus	2	2				1		dm	spr/aut	Х
Notiophilus palustris	2			1				dm	spr	h
Oodes helopioides	5	16		29	64	106	59	mac	spr	h
Ophonus diffinis						4	2	mac	aut	Х
Ophonus puncticeps					1			mac	spr/aut	х
Ophonus rufibarbis	18	11	1		13	23		mac	spr	Х
Oxypselaphus obscurus	33	31		31	44	64	161	dm	spr/aut	h
Panagaeus cruxmajor	1	1		1	7			mac	spr	h
Patrobus atrorufus	126	12	6	72	62	86	190	mac	spr	h
Philorhizus sigma		2				1		br	aut	h
Poecilus cupreus	285	478	1	308	285	160	796	mac	spr	h
Poecilus versicolor	1907	3149		89	1148	768	1318	mac	spr	е
Pterostichus anthracinus	61	56		85	85	139	223	dm	spr	h
Pterostichus diligens	8						2	dm	spr	h
Pterostichus gracilis	11	18		14	18	70	68	mac	spr	h
Pterostichus macer				1				mac	spr	h
Pterostichus melanarius	1021	1247	56	781	473	1388	3958	dm	aut	е
Pterostichus minor	1			1		1		dm	spr	h
Pterostichus niger	109	17	28	36	51	30	113	mac	aut	h
Pterostichus nigrita	5	5		12	14	10	18	dm	spr	h
Pterostichus rhaeticus	İ					1	1	br	spr	h
Pterostichus strenuus	47	46	1	4	129	73	19	dm	spr	h
Pterostichus vernalis	154	172		15	127	94	90	dm	spr	h
Stenolophus mixtus	3	36		6	11	27	11	mac	spr	h
Stenolophus skrimshiranus		3				25	241	mac	spr	h
Stomis pumicatus	13						1	dm	spr	h

Supplementary Material 1 5/5											
Species	Indiv	vidual	num	oers				Biolog	У		
	1998	8 1999 2002 2003 2004 2005 2006 flight repr hy									
Syntomus truncatellus	57	1					2	dm	spr	х	
Synuchus vivalis		10	1	1			18	dm	aut	х	
Tachys bistriatus	1						1	mac	spr	е	
Trechoblemus micros					1	1		mac	spr	h	
Trechus obtusus	69	88	1		28	17	9	dm	aut	h	
Trechus quadristriatus	181	113	1191	75	446	464	75	mac	spr/aut	е	
Zabrus tenebrioides				14	1			mac	aut	x	

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CHAPTER TWO 44 Appendices

this study: I – humi	d plot	ts wil	th lor	ng flo	od d	lurati	, on, Il	i – in	term	ediat	e plo	ts, II	I – d	ry pl	ots w	ith sl	hort f	100d	dura	tion.
90 <sup>-</sup> III					#					#					#					#
90 <sup>-</sup> II				#					#					#					#	
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5006		#					#					#					**			
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1_05			#					*					#					***		
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+0_II				#		es)			#					#					*	
1_04			#			anc		*					*					***		
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5003		***				trar	***					*					***			
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II <sup>-</sup> 05				**		zed,			***					* *		(th)			***	
I_02			***			urdiz		***					* * *			rersi		***		
5005		**				anda	**					**				a div	**			
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86 <sup>-</sup> II				#		uals			#					#		/er (				
86 <sup>-</sup> I	cies		*			ivid		#			sity		*			rnov				
866T	Spe	#				ind	#				iver	#				y tu				
	sr of					of of					b nd					unit				∞
	mbe	6	6	66	66	mbe	6	6	66	66	npsd	6	6	66	66	mm	98	9/98	36/66	6/66
	Nu	199	I_9	I	H	Nu	199	I_9		III	Sir	199	I_9	II II	III	Co	/66	I_9	II II	H

**Supplementary Material 2** Significance of the changes in standardized abundances, species richness, and community turnover among the sampling years. Differences of species numbers and abundances refer to the reference year 1999, whereas differences in community turnover refer to the reference condition of 1999/1998. (Wilcoxon test: # p > 0.05, # p < 0.05, # p < 0.01, # p < 0.001). Roman numerals refer to humidity classes used in this study: I – humid plots with long flood duration, II – intermediate plots, III – dry plots with short flood duration.

# CHAPTER THREE Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles

# Abstract

Environmental variability is the main driver for the variation of biological characteristics (lifehistory traits) of species. Therefore, life-history traits are particularly suited to identify mechanistic linkages between environmental variability and species occurrence and can help in explaining ecological patterns. For ground beetles, few studies directly related species traits to environmental variables. This study aims to analyse how life-history traits of alluvial ground beetles are controlled by environmental factors. I expected that the occurrence of species and the occurrence of specific traits are closely related to hydrological and disturbance parameters. Furthermore I expected most of the trait-variation to be explained by a combination of environmental variables, rather than by their isolated effects. Ground beetles were sampled in the year 2005 in floodplain grassland along the Elbe River in Germany. I used redundancy analysis to quantify the effects of hydrological, sediment, and disturbance related parameters on both species occurrence and species traits. I applied variation partitioning to analyse which environmental compartments explain most of the trait variation. Species occurrence and trait variation were both mainly controlled by hydrological and flood disturbance parameters. I could clearly identify reproductive traits and body size as key traits for floodplain ground beetles to cope with the environmental variability. Furthermore, combinations of hydrological, habitat disturbance, habitat type, and species diversity parameters, rather than their isolated effects, explained large parts of ground beetle trait variation. Thus, a main conclusion of this study is that ground beetle occurrence is mainly determined by complex, multi-scale interactions between environmental variability and their life-history traits.

**Keywords**: life-history traits, environmental variability, species sorting, trait shifts, floodplain, ecosystem processes

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# Introduction

Observing the occurrence of species and evaluating the response of biodiversity to changing environmental conditions is a major task of ecologists. With increasing ecological knowledge, however, the scientific focus shifted from purely observational to rather explanatory and predictive approaches. Recent attempts try to understand the observed occurrence patterns by focusing on the relationships between environmental variability and the life-history traits of organisms (Naeem & Wright 2003). Life history traits are biological characteristics of species allowing them to survive in their environments, including morphological, behavioural, and physiological characteristics (Lavorel & Garnier 2002). Current theory, like the habitat templet theory (Southwood 1988), predicts that species traits are mainly constrained by the environmental variability of their habitats and that abiotic factors act like filters, sorting organisms with unique trait combinations appropriate for specific habitat conditions (Statzner, Dolédec & Hugueny 2004). In the past years, several studies successfully applied this theory to determine or predict biodiversity effects of altering environmental conditions and showed the suitability of life-history traits for ecological research. For example, Dalgleish, Koons & Adler (2010) highlighted the usefulness of trait-based approaches to predict species vulnerability to climate change. Snyder (2008) noted that life-history traits can reveal how species can coexist and several studies described the effects of environmental variables on species traits (e.g. Pausas et al. 2004; Ilg & Castella 2006; Lehsten, Harmand & Klever 2008). The main conclusion of these studies is that functional traits of organisms can explain the ecological response of species (Lavorel et al. 1997). Thus, functional approaches can be seen as an extension of traditional ecological research, as they can reveal general assembly rules to explain ecosystem processes, and to give sound ecological interpretations.

Previously, such analyses were mainly applied to plants, but an increasing number of studies directly related environmental variables also to ground beetle life-history traits. Gobbi & Fontaneto (2008) noted that proportions of short winged, large and predatory species were negatively related to habitat disturbance. Similar results were found by Pizzolotto (2009) and Ribera *et al.* (2001), stressing that management intensity can influence trait dispersion and morphological characteristics of ground beetles, such as body size or wing morphology. For agricultural land-scapes Hendrickx *et al.* (2009) found that especially ground beetles with low dispersal ability are threatened by habitat fragmentation and Lambeets *et al.* (2008) demonstrated multiple trait shifts of ground beetles along gradients of flood disturbance. The main conclusion of all these studies is that life-history traits of ground beetles are strongly affected by a variety of different environmental variability in a large range of different habitats.

Analyzing trait-environment relationships is especially suitable in naturally dynamic landscapes, because this allows for observing biological patterns without elaborately manipulate environmental conditions (Henle *et al.* 2006). Floodplains provide exceptional opportunities for such kind of research, since the episodic alternation of floods and droughts causes high spatio-temporal habitat heterogeneity (Tockner & Stanford 2002), being one of the most important drivers for species assemblages and the high species richness of these ecosystems (Adis & Junk 2002). Floodplain faunal species are therefore expected to display a large range of adaptations and strategies to cope with varying environmental conditions (Robinson *et al.* 2002). However, given this high biotic and abiotic variety of floodplains, mechanistic linkages between environmental variability and life-history traits of organisms are difficult to reveal and thus still insufficient-

Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles

ly understood. This is to some degree also true for ground beetles, although they are one of the best studied, most species rich and abundant macroinvertebrate taxon in terrestrial and semi-terrestrial habitats and particularly suitable for the investigation of species-environment relationships (Lövei & Sunderland 1996; Rainio & Niemelä 2003). Recently, some considerable progress has been made to identify the life-history traits of ground beetles to understand their response to floodplain dynamics. Most of the species are good flyers, which enables them to actively evade rising floodwaters and to quickly recolonize the habitats after flooding (Desender 1989). Additionally, a huge amount of alluvial ground beetles are habitat generalists (Weigmann & Wohlgemuth-von Reiche 1999), which may increase the chance of finding surrogate habitats and to quickly recolonize habitats after flooding. The adults of several alluvial species can stay submerged for a considerable time period and are thus able to outlast flood events for a certain time in the floodplain (Siepe 1989; Rothenbücher & Schaefer 2006). In contrast, ground beetle larvae are rather intolerant to hydrological stress (Den-Boer & Den-Boer-Daanje 1990) and therefore many alluvial species develop in less flood exposed habitats (Rothenbücher & Schaefer 2006). Spring reproduction is another crucial strategy to ensure reproductive success in these highly dynamic floodplain habitats. Early reproduction enables the larvae to develop during summer, which is usually a period of low hydrological disturbance, and thus can decrease larval mortality and increase reproductive success (Thiele 1977).

Despite the general knowledge of ground beetle survival strategies in floodplains, it is yet not clear how environmental variability controls the distribution of particular traits within species assemblages. Bates *et al.* (2006) and Lambeets *et al.* (2008) gave some first insight, as they directly related floodplain variables to specific life-history traits of the species. They stressed the importance of flood disturbance and soil conditions on the variation of species traits. However, these studies were conducted on river banks, being characterized by an extremely high disturbance regime with rapidly altering environmental conditions. For other habitats, like less disturbed floodplain grasslands, other parameters might be of greater importance for the species. The primary aim of this study is to explain the occurrence of ground beetles by linking species life-history traits with environmental variability and species and the variation of their traits are strongly affected by hydrological and disturbance related parameters. Due to the environmental complexity of floodplain habitats I further hypothesize that most of the trait variation will be explained by a combination of different environmental variables, rather than by their isolated effects.

Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles

### Methods

### Study area

The study was conducted at the UNESCO Biosphere Reserve "Elbe River Landscape" in Central Germany at the Elbe River. With a length of about 1,100 km and a catchment area of about 150,000 km2 the Elbe River is the third largest stream in Germany and ranks among the largest streams in Europe. The mean annual discharge of the Elbe River ranges from 336 m3/s upstream to 730 m3/s downstream. The water level is mainly dominated by snow-melt in spring and erratic precipitation over the year, inducing high discharge in winter and spring, and low discharge in summer. In general, flood regime and floodplain habitats of the Elbe River in Central Germany can be considered close to the natural state (Scholten *et al.* 2005).

The survey was carried out in the year 2005 on 36 plots located in seasonally flooded grasslands. The study site is located near the village of Steckby, close to Dessau town in the state of Saxony-Anhalt. The plots were located following a stratified, randomised design. For this, the study site was subdivided into three habitat types regarding vegetation and soil morphology: floodchannels, humid grasslands and mesophilous grasslands. The sampling plots were then randomly located within each of the three habitats (see Henle et al. 2006 for a detailed description of the study design). The study site is characterised by a mosaic of higher and lower areas, which are differently exposed to floods (Fig. 1), whereas the more elevated and dryer areas were cut twice a year and the lower ones (e.g., floodchannels) were spared from utilisation. On each plot five pitfall traps were installed and filled with a 7% solution of acetic acid and a detergent to reduce surface tension. The traps were exposed from May to June and from September to October with a trap exposure time of 28 days per period. All adults were determined to species level and stored in a solution of two-thirds ethanol (70 %) and one-third acetic acid (30 %).



**Figure 1** Grassland habitats displaying different hydrological conditions in the study site Steckby. Copyright: Mathias Scholz (UFZ, Leipzig).

### Life-history traits

Information on the life-history traits of ground beetles were queried from a self-compiled database. The included trait data came from standard references on Central European ground beetles, mostly determination keys and ground beetle compendia. Altogether 18 traits with 60 trait categories, ranging from biological and morphological to ecological characteristics, were included in the database. For this study I used 8 traits and 25 trait categories to describe the effects of environmental variables on the variation of the traits. See Table 1 and Appendix I for an overview of the traits included in the database and the ones used in this study including the references used to compile the database. To obtain a rectangle traits-by-site matrix that can be analysed by multivariate statistics, the number of individuals possessing a particular trait category (e.g. spring breeders) was allocated to each plot, similarly to an ordinary species-by-site matrix (i.e. species were replaced by trait categories). If individuals shared more than one trait category, e.g. dimorphic species, they received an entry for each category.

Table I Life history dats of ground	i beeties used in this study.	
Trait	Trait categories	comments
Body size	1 – diminutive	< 3.0 mm
	2 – very small	3.1 – 6.0 mm
	3 – small	6.1 – 10.0 mm
	4 – medium	10.1 – 19 mm
Wing morphology	1 – macropterous	
	2 – brachypterous	
Season of reproduction	1 – spring	From February to June
	2 - autum	From July to Oktober
Hatching season	1 – spring	
	2 – atumn	
Overwintering type	1 – as imago	
	2 – as larvae	
Daily activity	1 – diurnal	
	2 – nocturnal	
Body pubescence	1 – head	
	2 – pronotum	
	3 – elytra	
	4 – hairless	
Food strategy	1 – opportunistic carnivores	
	2 – specialized carnivores	
	3 – phytophagous	
	4 – polyphagous	

### Environmental variables

In the years 1998 and 1999, dipwell and crest gauges were installed on each sampling plot to measure maximum groundwater depth (in m), mean groundwater depth (in m), duration of inundation (in weeks), and inundation height (in m). Follner and Henle (2006) correlated these plot-measurements with data from official Elbe gauges near the study site Steckby, which are daily collected by the German Waterways and Shipping Administration. By additionally accounting for evapotranspiration, a hydrological model was set up to calculate the selected hydrological variables (see Table 2) even for the year 2005, although hydrological field measurements did not continue after 1999. The reliability, the temporal and statistical robustness, as well as the application of this hydrological model was recently tested and approved in the framework of developing a bioindicator system for ecological changes in floodplains (Follner *et al.* 2009). Soil substrate data came also from the survey in 1999, but as the substrate type of the sampling plots did not change during the 6-year time span, I used this data for the analyses as well.

	lables asea in this study.		
Variable	Description	Scale unit	Compartment
Flood.height.max	Maximum flood height	Continous (cm)	Disturbance
Flood.nr/year	Number of floods per year	Continous (no.)	Disturbance
Flood.duration	Flood duration	Continous (weeks)	Disturbance
Gw.level.max	Maximum ground water depth	Continous (cm)	Hydrology
Gw.level.mean	Mean groundwater depth	Continous (cm)	Hydrology
Gw.level.varcoef	Variation coefficient of groundwater depth	Continous (no dimension)	Hydrology
Substrate.loam	Loamy substrate	Binary (0 = no, 1 = yes)	-
Substrate.sand1	Sandy Substrate (< 90 % sand amount)	Binary (0 = no, 1 = yes)	-
Substrate.sand2	Sand (> 90 % sand amount)	Binary (0 = no, 1 = yes)	-
Substrate.silt	Silty substrate	Binary (0 = no, 1 = yes)	-
Management.mown	Habitat mown	Binary (0 = no, 1 = yes)	Disturbance
Management.unused	No management	Binary (0 = no, 1 = yes)	Disturbance
Habitat.floodchannel	Habitat type floodchannel	Binary (0 = no, 1 = yes)	Habitat
Habitat.meadow.medium	Habitat type mesophilos grassland	Binary (0 = no, 1 = yes)	Habitat
Habitat.meadow.humid	Habita type humid grassland	Binary (0 = no, 1 = yes)	Habitat

 Table 2
 Environmental variables used in this study.

### Data analysis

Ecological studies are often biased by spatial autocorrelation, i.e. closely located samples are not independent because they can share attributes of their neighbouring samples (Dormann *et al.* 2007). However, independence of data points is a crucial assumption for most statistical methods. To identify spatial autocorrelation of ground beetle species richness, relative abundances and Simpson's diversity I used Moran's *I*, which is a weighted correlation coefficient that detects spatial randomness or spatial clustering of variables. Values being larger than zero show positive, and values less than zero indicate negative spatial dependence of the variables. I used the knearneigh-function of the R-package spdep using 6 plots as nearest neighbours to calculate the spatial weights matrix. Statistical significance of the autocorrelation was tested with saddlepoint approximation tests.

Principal Component Analysis (PCA) was conducted i) to identify the most important environmental variables and ii) to exclude highly correlated variables prior to further analyses. Since the environmental variables were measured on different scale units (see Table 2), I standardised them to a zero mean and unit variance to equally weight the variables. Data for substrate, management intensity, and habitat type were categorical. Therefore, these variables were transformed into dummy coded binary data before included into the analysis.

I aimed to assess the influence of environmental variables on both species assemblages and on particular species traits. A preliminary Detrended Correspondence Analysis revealed very short gradient lengths of the species and the trait datasets, suggesting low turnover rates of species and traits among the axis-gradient and thus a linear response. Therefore, I performed Redundancy Analysis (RDA) on the species (which is referred to as "species-RDA" in the following) and the traits dataset ("trait-RDA"), being much better suited for linear response patterns than unimodal models like Canonical Correspondence Analysis (Lepš and Smilauer 2003). I compared the RDA models (i.e. ordination constrained by environmental variables) with unconstrained PCA models to identify the relative influence of environmental factors on the ordination models.

To determine the degree to which the occurrence of species and the occurrence of particular species traits are correlated, I performed a Procrustes rotation analysis on the species and the trait dataset. Procrustes rotation aims to find maximal congruency, i.e. similarity of data points, between two ordination models by rotating, expanding and rescaling an ordination model towards a target ordination (Legendre and Legendre 1998). To estimate if environmental variables affect the correlation I performed two Procrustes rotations: i) without environmental variables, i.e. rotation of a species-PCA model against a trait-PCA model, and ii) constrained by environmental variables, i.e. a rotation of a species-RDA model and a trait-RDA model. Statistical significance of the Procrustes rotation models were tested with a randomization test with 9,999 permutation iterations.

Variation partitioning was then used to separate the effects of different environmental compartments (predictor variables) on the variation of ground beetle life-history traits (response variable). Variation partitioning is based on RDA and tries to identify how successful a set of different predictor variables is at explaining the response variable (Legendre 2008). Hereby, the total percentage of variation explained by an RDA-model is partitioned into unique and common contributions of the predictor variables. I assumed variables related to hydrology and disturbance to explain most of the trait variation. Therefore, I divided the environmental dataset into

a "hydrology" and a "disturbance" compartment (see Table 2). I additionally created a "habitat" compartment to account for the effects of environmental variables that were not measured, but being reflected in the habitat type, such as soil moisture, pH value, nutrient content etc. I assumed that species rich ground beetle assemblages should explain large parts of the trait-variation, because they should contain a large proportion of species with different biological characteristics. To account for these effects, I set up a "species diversity" compartment, containing species richness and Simpson's diversity. Since preliminary analyses showed that soil substrate did not explain any variation in the trait-data, I excluded the soil compartment from variation partitioning.

Relative abundances of the individuals were log-transformed to reduce the skew in the data. All statistical analyses were performed with the packages vegan (version 1.15-4), spdep (version 0.4-54), and ade4 (version 1.4-14) in the R environment (R Development Core Team 2010).

# Results

Overall, 26, 557 individuals from 107 species were sampled. *Agonum emarginatum* (Gyllenhal 1827; 27.7%) and *Poecilus versicolor* (Sturm 1824; 12.4%) made out 40% of the overall individual density. 38 species were recorded with less than 5 individuals, including some stenotopic alluvial species like *Agonum dolens* (Sahlberg 1827), *Bembidion argenteolum* (Ahrens 1812) and *Omophron limbatum* (Fabricius 1776). See Appendix II for a full species list. I found only minimal spatial autocorrelation of Simpson's diversity, as seen by the relatively low Moran's I value (M), which was only slightly greater than zero (M = 0.178, p = 0.015) (Table 3). Spatial dependency of both species richness (M = 0.292, p = 0.001) and species abundances (M = 0.394, p < 0.001) was little higher, nevertheless indicating a minor role of spatial autocorrelation in this study.

Table 3         Spatial Autocorrelation base	ed on Moran's I.	
Metric	Moran's I	р
Species richness	0.292	0.001
Species abundances	0.394	< 0.001
Simpson's diversity	0.178	0.015

To reduce the complexity of the subsequent models by excluding highly correlated data, I conducted a PCA on the full environmental dataset. The full PCA model explained 68.4% (F1: 49.4, F2: 19.3) of the total variance in the environmental data, but due to collinearity I excluded 10 environmental variables from this model (abbreviations see Table 1): gw.level.max, flood.height. max, flood.duration, gw.level.varcoef, substrate.silt, substrate.sand2, management.unused, habitat.floodchannel, habitat.meadow.medium, habitat.meadow.humid. The reduced model consisted of 5 variables and explained 79.7% of the variation of the remaining environmental data (F1: 44.1%, F2: 35.6%). The sampling plots were ordinated along gradients of hydrolo-

### CHAPTER THREE 53 Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles

gical, habitat disturbance, and soil parameters (Fig. 2). Plots on the first PCA axis were mainly influenced by habitat management as well as flood and groundwater related variables, whereas soil type was the most important factor on the second axis. There are three groups of plots with similar environmental conditions, which clearly refer to the habitat types defined prior to the analyses. Habitats located in floodchannels were strongly influenced by the mean groundwater depth, whereas humid grassland habitats were more affected by the numbers of floods. The driest plots have also the highest amount of sand and are mown once or twice a year, compared to the unused floodchannels.



the different habitat types: Black = floodchannels, grey = mesophilous grassland, white = humid grassland.

To evaluate how environmental variables affected the composition of species and traits I performed a Redundancy Analysis (RDA) with the reduced environmental dataset on the species and the trait dataset. The first two axes of the species-RDA explained 58.54% of the variance in the species dataset (F1: 54.00%, F2: 5.84%, Fig. 3A). It is obvious that mainly management and hydrological variables, such as the mean groundwater depth, are the main drivers affecting species occurrence. Mainly hygrophilous alluvial species, such as *Agonum* or *Bembidion* species, but also *Oodes helopioides* (Fabricius 1792) and *Pterostichus anthracinus* (Illiger 1798) are related with these environmental conditions. Therefore, plots possessing a high proportion of alluvial

Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles

species were ordinated on the left side of the diagram. In contrast, the most ubiquitous species, like *Pterostichus melanarius* (Illiger 1798), *Poecilus versicolor* (Sturm 1824) and *Nebria brevicollis* (Fabricius 1792), as well as xerophilous species like *Amara equestris* (Duftschmid 1812) were rather correlated with increasing human management and higher groundwater levels and thus ordinated to the right side of the diagram. Because of the low explanatory power of the second RDA axis, soil type has only little impact on species occurrence patterns.



**Figure 3** Relationship between environmental variables and species occurrence A and occurrence of species traits B by means of Redundancy Analysis. Points represent the sampling plots. Species scores omitted due to clarity. The colors indicate the habitat type of the sampling plots: black = floodchannels, grey = mesophilous grassland, white = humid grassland. Traits and species that accounted most for the explained variance along the first RDA axis are plotted in italics.

The first two axes of the trait-RDA explained 64.35% of the total trait variance in the dataset (F1: 59.90%, F2: 4.45%, Fig. 3B). The results indicate that especially reproductive traits and body size are strongly affected by the disturbance regime and by the hydrology of the habitats. On the left side of the ordination diagram, plots are located with a high amount of individuals reproducing in spring and hatching in summer. Most of them are additionally small sized species. On the contrary, summer/autumn breeding species and larger species are plotted more on the right side of the diagram.

Procrustes rotation analysis showed a significant correlation between species ordination and trait ordination, relatively independent from the presence of environmental constraints in the ordination (Table 4). This shows that sampling plots with a unique species composition also possess organisms with specific life-history traits. The PCA models (ordination of species and traits is not constrained by environmental variables) showed a higher congruency between each other, whereas the rotation of the RDA models tended to be less precise and showed a large part of unexplained variance, evident from the RSS values four times higher than those from the PCA model rotation.

# Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles

	Not constrained by environmental variables (PCA)	Constrained by environmental variables (RDA)
Correlation coefficient	0.69	0.61
Residual Sum of squares	20.37	82.73
Root mean squared error	0.12	0.13
p-value	< 0.001	< 0.001

 Table 4
 Parameters of Procrustes rotation analysis of species and trait datasets.

The environmental compartments hydrology, disturbance, habitat type and species diversity explained 72 % of the overall variation of the ground beetles life-history traits (Fig. 4). However, partitioning the effects of the predictor variables on ground beetle trait variation revealed only little explanatory power of each environmental compartment separately. Hydrology alone explained the largest part and diversity and disturbance explained the smallest part of the overall variation. The unique contribution of all compartments to the overall trait variation was 22 %, whereas the common contribution (i.e. the combination of all compartments) was about 50 %. In other words, the different environmental compartments explained to large degrees similar parts of the trait variation, indicating a certain amount of explanatory redundancy in the predictor variables.



**Figure 4** Partitioning the effects of four environmental compartments hydrology, disturbance, habitat type, and species diversity on the variation of ground beetle life-history traits. See Table 1 for a description of the variables included in each compartment. Values < 0.03 are not shown.

### Discussion

This study tackles the problem of identifying mechanistic linkages between environmental variability, biotic characteristics of organisms and the occurrence of species in dynamic landscapes. Here I show that both species occurrence and the variation of ground beetle life-history traits are controlled by similar environmental variables. Reproductive traits and body size were found to be key traits of floodplain ground beetles enabling them to cope with management intensity and groundwater depth. Furthermore, combinations of hydrological, habitat disturbance, habitat type, and species diversity parameters, rather than their isolated effects, explained large parts of ground beetle trait variation. A main conclusion of this study is therefore that ground beetle occurrence in floodplain grasslands is mainly determined by complex interactions between environmental variability and specific life-history traits.

### Environmental effects on species traits

Management intensity, groundwater depth, and to a lesser degree soil substrate were the most important environmental variables driving the occurrence of species and the variation of ground beetle traits. Previous work on ground beetles in floodplains highlighted the importance of environmental variables for species occurrence in these dynamic habitats. For riverbanks, being considered as the most disturbed habitats in floodplains, Eyre & Luff (2001), Kleinwächter & Rickfelder (2007) and Framenau *et al.* (2002) noted that sediment type and flood disturbance are the most important factors affecting the occurrence of ground beetles. In this study I revealed that sediment type had only little influence on species occurrence and trait variation. This was not surprising, as soil dynamics, e.g. sediment erosion or deposition, are relatively low in floodplain grasslands and might therefore not be of primary importance for grassland arthropods. Rather than soil variables I found that habitat disturbance and hydrological parameters are the main factors that drive the occurrence of ground beetles in the study site. This is coincident with studies of Antvogel & Bonn (2001) and Gerisch *et al.* (2006) stating that flood duration, groundwater depth and habitat management are the main factors influencing the occurrence of ground beetles in the study site.

However, species occurrence patterns are often distance related, i.e. the values of variables (species, individuals) sampled at nearby locations are not independent from each other, which is also known as spatial autocorrelation (Legendre & Legendre 1998; Dormann *et al.* 2007). The relatively low Moran's I values in this analysis indicate that ground beetles were rather dispersed than clustered within certain habitat types. This means that the differences in species diversity are not primarily due to spatial proximity of the sampling plots, but mainly caused by environmental variability and habitat configuration. Nevertheless, there is obviously a relationship between species assemblages located close together.

The results indicate that species assemblages of certain habitat types share unique combinations of traits, which clearly confirms the habitat templet theory. The importance of hydrological and disturbance parameters for wetland ground beetle traits is well documented in the literature. Thiele (1977) stressed the importance of floodplain species to reproduce in spring to avoid flood disturbance. Eyre & Luff (2001) suggested that small body size and high mobility enable floodplain ground beetles to quickly respond to increasing disturbance. Bates *et al.* (2006) and Lambeets *et al.* (2009) confirmed these assumptions, showing that several life-history traits of riverbank spiders and ground beetles are strongly affected by flood disturbance parameters.

According to Ribera *et al.* (2001), Sadler *et al.* (2006) and Lambeets *et al.* (2008), disturbance mainly affects the dispersal capacity and the body size of ground beetles. Hence, a small body size and fully developed wings enable species to quickly evade the disturbance or quickly recolonize the disturbed plots. Overall, it is not surprising that both, the occurrence of species and their particular traits, are affected by similar environmental variables. It is suggested that only certain traits enable organisms to cope with environmental variability or extreme environmental conditions (Townsend *et al.* 1997). Obviously, the set of suitable traits for coping with environmental stress is limited by nature. Therefore, "successful" strategies can be shared by several species simultaneously. The rising question of species coexistence can be best explained with functional redundancy (Petchey *et al.* 2007; Flynn *et al.* 2009) and flexible niche partitioning (Finke & Snyder 2008). This means, species possessing similar life-history traits (i.e. being functionally redundant) are still able to coexist in the same habitat, because species resource use behavior is expected to be plastic to minimize competition. Unfortunately, there are no ground beetle studies addressing functional redundancy issues, which is why an increased research on those topics is crucial to verify these assumptions.

### Combined environmental effects on species traits

Partitioning the effects of environmental variables clearly showed that a combination of all four compartments hydrology, habitat disturbance, habitat type, and species diversity explained the largest part of the overall trait variation. However, this does not automatically mean that each compartment separately is unimportant for ground beetles. In fact, each environmental compartment explained unique parts of the ground beetle trait variation, although to a comparable little amount. For example, flood disturbance is closely connected to hydrological parameters, i.e. frequently flooded plots are often the ones with the lowest groundwater depth. However, hydrological factors might not necessarily have similar impacts on the trait variation than habitat disturbance parameters. Habitat disturbance primarily affect morphological characteristics of the species, like wing morphology or body size (Ribera et al. 2001; Lambeets et al. 2009). In contrast, the alternation of hydrological parameters might more relate to reproductive traits, as shown in this study. This is also supported by Cárdenas & Hidalgo (2007) who note that although most ground beetles in floodplains are spring breeders, also autumn breeding can take place at the more elevated plots. They also state that reproduction in spring might be a useful strategy for floodplain ground beetles to avoid hydrological stress for their larvae, as soil humidity in floodplains decreases considerably during the summer. I thus assume that hydrology explains mainly the variation of reproductive traits, while habitat disturbance parameters explain large parts of dispersal related traits of floodplain ground beetles. Nevertheless, the relatively high explanatory redundancy of the predictor variables suggests that there are other important variables affecting the variation of ground beetle life-history traits.

# Conclusions

This study confirms current knowledge about (pre-)adaptations of alluvial ground beetles to floodplain dynamics. As is evident from previous work, traits related to dispersal and reproduction are the most affected ones by flooding and are shown to change strongly with increasing inundation. This trait variation is best explained by a combination of different abiotic variables, indicating that ground beetle life-history traits are affected by multiple environmental stressors. Consequently, future ecological work and floodplain conservation measures should both focus on different facets to maintain the high trait diversity of alluvial ground beetles and the ecological functions they have in ecosystems.

Based on this work I can conclude that life-history traits can be used to predict the occurrence of organisms with certain biological characteristics to altering floodplain dynamics and to better understand ecological patterns (i.e. species occurrences). Therefore, combining traditional taxonomic approaches with current trait-based approaches is a great chance to reveal ecosystem processes and identify "rules" describing how organisms interact with their dynamic environments. Due to the high variety of different traits and strategies to cope with habitat dynamics, I appeal to intensify the application of trait-analyses also for ground beetles to increase our knowledge on processes affecting carabid-environment relationships.

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# Appendices

Туре	Trait Number	Trait category Number	Trait	Trait category	Used in this study
	101	10101	body size	diminutive	X
	101	10102	body size	very small	x
	101	10103	body size	small	х
	101	10104	body size	medium	x
	101	10105	body size	large	
	101	10106	body size	very large	
	102	10201	wing morphology	macropterous	x
	102	10202	wing morphology	brachypterous	x
	103	10301	reproduction period	spring/early summer	x
	103	10302	reproduction period	summer/autumn	x
	104	10401	hatching season	spring/early summer	
	104	10402	hatching season	summer/autumn	
	105	10501	overwintering stage	larvae	x
	105	10502	overwintering stage	imago	x
	106	10601	daily activity	diurnal	x
	106	10602	daily activity	nocturnal	x
tic	107	10701	color head	black	
eris	107	10702	color head	brown/black brown/red-brown	
act	107	10703	color head	red/yellow-red	
har	107	10704	color head	yellow/yellow-brown	
alc	107	10705	color head	metallic (greenish-bluish)	
ent	107	10706	color head	metallic (gold-coppery)	
md	108	10801	color pronotum	black	
velo	108	10802	color pronotum	brown/black-brown/red-brown	
dev	108	10803	color pronotum	red/yellow-red	
cal,	108	10804	color pronotum	yellow/yellow-brown	
ts	108	10805	color pronotum	metallic (greenish-bluish)	
hol	108	10806	color pronotum	metallic (gold-coppery)	
rd i orp	109	10901	color elytra	black	X
Ia	100	10002	color elvtra	brown/black-brown/red-brown	v

Append	ix I 2/2				
Туре	Trait Number	Trait category Number	Trait	Trait category	Used in this study
	109	10903	color elytra	red/yellow-red	x
	109	10904	color elytra	yellow/yellow-brown	х
	109	10905	color elytra	metallic (greenish-bluish)	х
	109	10906	color elytra	metallic (gold-coppery)	
tics	110	11001	elytra pattern	no pattern	
eris	110	11002	elytra pattern	Pattern darkened	
act	110	11003	elytra pattern	Pattern pale	
har	111	11101	color legs	darkened	
alc	111	11102	color legs	pale	
lent	111	11103	color legs	metallic	
ude	112	11201	body pubescence	head	х
velo	112	11202	body pubescence	elytra	х
dev	112	11203	body pubescence	pronotum	х
cal,	112	11204	body pubescence	hairless	х
lts logi	113	11301	food type	opportunistic carnivores	х
trai	113	11302	food type	specialised carnivores	x
urd	113	11303	food type	phytophagous	x
H <sup>a</sup> (m	113	11304	food type	polyphagous	х
	201	20101	humidity preference	hygrophilous	
	201	20102	humidity preference	xerophilous	
	201	20103	humidity preference	mesophilous	
	202	20201	light preference	unshaded	
tics	202	20202	light preference	partly shaded	
eris	202	20203	light preference	mainly or fully shaded	
cat	203	20301	salt tolerance	yes	
har	203	20302	salt tolerance	no/unknown	
s al c	204	20401	habitat preference	wooden habitats	
rait	204	20402	habitat preference	open habitats	
fit ti cole	205	20501	habitat specialisation	stenotopic	
So (E	205	20502	habitat specialisation	eurytopic	

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Species	Author	Habitat typ	Habitat type		
		flood- channels	humid grassland	mesophilous grasland	
Acupalpus dubius	Schilsky 1888	1	1	0	
Acupalpus exiguus	Dejean 1829	62	15	37	
Acupalpus parvulus	Sturm 1825	5	0	0	
Agonum dolens	CR Sahlberg 1827	2	0	0	
Agonum duftschmidi	Schmidt 1994	587	6	340	
Agonum emarginatum	Duftschmid 1812	3239	39	4071	
Agonum fuliginosum	Panzer 1809	2	0	4	
Agonum lugens	Duftschmid 1812	11	0	0	
Agonum marginatum	Linné 1758	23	0	0	
Agonum micans	Nicolai 1822	476	52	671	
Agonum piceum	Linné 1758	19	2	8	
Agonum sexpunctatum	Linné 1758	0	0	2	
Agonum thoreyi	Dejean 1828	1	0	0	
Agonum versutum	Sturm 1824	325	9	39	
Amara aenea	De Geer 1774	1	8	0	
Amara aulica	Panzer 1797	0	1	3	
Amara bifrons	Gyllenhal 1810	0	1	0	
Amara communis	Panzer 1797	69	39	123	
Amara equestris	Duftschmid 1812	1	40	0	
Amara familiaris	Duftschmid 1812	3	5	6	
Amara lunicollis	Schiödte 1837	16	75	15	
Amara ovata	Fabricius 1792	2	4	3	
Amara plebeja	Gyllenhal 1810	5	5	4	
Amara similata	Gyllenhal 1810	4	3	2	
Amara strenua	Zimmermann 1832	1	79	6	
Amara tibialis	Paykull 1798	1	1	1	
Anisodactylus binotatus	Fabricius 1787	285	49	94	
Anthracus consputus	Duftschmid 1812	192	19	37	
Badister bullatus	Schrank 1798	0	1	0	
Badister meridionalis	Puel 1925	2	1	0	

**Appendix II** 1/4 Recorded species of the study, separated by the main habitat type. Numbers represent individual numbers.

Appendix II 2/4				
Species	Author	Habitat type		
		flood- channels	humid grassland	mesophilous grasland
Badister sodalis	Duftschmid 1812	0	0	7
Badister unipustulatus	Bonelli 1813	7	1	0
Bembidion argenteolum	Ahrens 1812	1	0	0
Bembidion assimile	Gyllenhal 1810	14	1	8
Bembidion azurescens	Dalla Torre 1877	0	0	2
Bembidion biguttatum	Fabricius 1779	340	15	157
Bembidion dentellum	Thunberg 1787	343	14	69
Bembidion fumigatum	Duftschmid 1812	2	0	1
Bembidion gilvipes	Sturm 1825	21	12	6
Bembidion guttula	Fabricius 1792	33	228	88
Bembidion lunulatum	Geoffroy in Fourcroy 1785	4	0	0
Bembidion minimum	Fabricius 1792	1	0	0
Bembidion octomaculatum	Goeze 1777	1	0	1
Bembidion properans	Stephens 1828	0	1	1
Bembidion quadrimaculatum	Linné 1761	2	0	0
Bembidion semipunctatum	Donovan 1806	4	0	0
Bembidion tetracolum	Say 1823	1	1	0
Bembidion varium	Olivier 1795	1	0	0
Blethisa multipunctata	Linné 1758	7	1	6
Bradycellus harpalinus	Audinet-Serville 1821	0	1	0
Calathus fuscipes	Goeze 1777	0	92	1
Calathus melanocephalus	Linné 1758	8	36	0
Carabus auratus	Linné 1761	0	2	0
Carabus glabratus	Paykull 1790	0	1	11
Carabus granulatus	Linné 1758	788	508	820
Carabus nemoralis	OF Müller 1764	1	2	0
Chlaenius nigricornis	Fabricius 1787	380	20	121
Chlaenius tristis	Schaller 1783	0	0	1
Clivina fossor	Linné 1758	349	192	229

Species	Author	Habitat typ	Habitat type		
		flood- channels	humid grassland	mesophilous grasland	
Cychrus caraboides	Linné 1758	0	0	1	
Demetrias monostigma	Samouelle 1819	3	0	2	
Dyschirius aeneus	Dejean 1825	3	0	1	
Dyschirius globosus	Herbst 1784	7	7	16	
Dyschirius luedersi	Wagner 1915	16	0	0	
Elaphrus cupreus	Duftschmid 1812	15	10	9	
Elaphrus riparius	Linné 1758	9	1	0	
Epaphius secalis	Paykull 1790	1	2	41	
Harpalus distinguendus	Duftschmid 1812	0	2	0	
Harpalus latus	Linné 1758	3	11	14	
Harpalus luteicornis	Duftschmid 1812	7	3	2	
Harpalus signaticornis	Duftschmid 1812	1	1	0	
Loricera pilicornis	Fabricius 1792	211	142	266	
Microlestes minutulus	Goeze 1777	0	1	0	
Nebria brevicollis	Fabricius 1792	87	1564	6	
Notiophilus aquaticus	Linné 1758	0	1	0	
Notiophilus palustris	Duftschmid 1812	0	3	0	
Odacantha melanura	Linné 1767	1	0	0	
Omophron limbatum	Fabricius 1776	1	0	0	
Oodes helopioides	Fabricius 1792	180	10	165	
Oxypselaphus obscurus	Herbst 1784	29	5	39	
Patrobus atrorufus	Stroem 1768	43	0	6	
Philorhizus sigma	P Rossi 1790	2	0	2	
Platynus assimilis	Paykull 1790	14	5	0	
Platynus livens	Gyllenhal 1810	3	0	3	
Platynus longiventris	Mannerheim 1825	1	0	0	
Poecilus cupreus	Linné 1758	168	172	88	
Poecilus versicolor	Sturm 1824	179	2659	452	
Pseudoophonus rufipes	De Geer 1774	6	11	5	
Pterostichus anthracinus	Illiger 1798	370	43	330	
Pterostichus diligens	Sturm 1824	2	0	3	

Appendix II 4/4				
Species	Author	Habitat type		
		flood- channels	humid grassland	mesophilous grasland
Pterostichus gracilis	Dejean 1828	305	14	221
Pterostichus melanarius	Illiger 1798	40	583	61
Pterostichus minor	Gyllenhal 1827	6	0	5
Pterostichus niger	Schaller 1783	7	1	9
Pterostichus nigrita	Paykull 1790	238	26	226
Pterostichus rhaeticus	Heer 1838	1	0	1
Pterostichus strenuus	Panzer 1797	31	63	125
Pterostichus vernalis	Panzer 1796	53	22	34
Stenolophus mixtus	Herbst 1784	325	3	73
Stenolophus skrimshiranus	Stephens 1828	52	0	32
Stomis pumicatus	Panzer 1796	0	0	1
Syntomus truncatellus	Linné 1761	0	5	1
Tachys bistriatus	Duftschmid 1812	14	0	0
Trechoblemus micros	Herbst 1784	1	0	0
Trechus obtusus	Erichson 1837	3	11	0
Trechus quadristriatus	Schrank 1781	51	183	41
Trichocellus placidus	Gyllenhal 1827	0	0	2

# CHAPTER FOUR More species, but all do the same – Contrasting effects of ground beetle species and functional diversity to flood disturbance

# Abstract

The role of habitat disturbance on biodiversity is central as it promotes changes in ecological systems. That said, still little is known about the functional consequences of such changes. Functional diversity can be used to revealing more mechanistically the disturbance effects on communities by considering the richness and the distribution of traits among the species. Here we analyzed the response of functional and species diversity of ground beetles to flood disturbance to better understand the functioning of alluvial invertebrate communities. Ground beetles were sampled in periodically flooded grasslands along the Elbe River in Germany. We used generalized linear mixed effects models to unveil the relationships between flood disturbance, species and functional diversity, respectively. We measured different components of functional diversity (functional richness, evenness, dispersion, and divergence) and analyzed species diversity by means of rarefied species richness, abundances, evenness and Simpson's diversity. We found contrasting relationships in that most species diversity measures peaked at highest disturbance levels, while most functional diversity measures decreased with increasing disturbance intensities. Inversed relationships between species and functional diversity are rarely observed, as most studies report on positive correlations. We explain increasing species diversity with a higher amount of resources available in highly disturbed sites. Decreasing functional diversity is best explained through the convergence of species traits by flood disturbance and uneven resource exploitation in highly disturbed plots (low functional evenness), suggesting strong impacts from functionally different generalist species in floodchannels. We show that the amount of resources available, and how these resources are exploited, play major roles in the functioning of floodplain ground beetle communities.

Keywords: assemblages, carabids, habitat-templet, species sorting, environmental filtering

This chapter has been published as

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**CHAPTER FOUR** 69

# Introduction

Disturbance is one of the key drivers structuring ecological communities and a major agent in governing the functioning of ecosystems (Hooper *et al.* 2005; Díaz *et al.* 2007). It regulates species diversity through the generation of habitat heterogeneity, induces species turnover and, hence, community dynamics (Death 2002; Hughes *et al.* 2007; Ilg *et al.* 2008a). Ultimately, habitat disturbance is seen as one of the most important variables shaping the life-history traits and the survival strategies of organisms in fluctuating environments (Lytle 2001). The relations-hips between habitat disturbance and species diversity have been an active research field for decades, but discussions as to whether species diversity alone can effectively explain respectively predict the response of biodiversity to disturbance are still ongoing (Cadotte 2007). A weak point of traditional species diversity measures is that they do not integrate the biological differences among the species and therefore cannot fully reflect the linkages between environmental fluctuation, species occurrence, and community processes. Within these discussions the concept of functional diversity (FD) emerged as a tool to analyze the various ways organisms respond to environmental variability and to better understand the functioning of ecological communities, for example after disturbances (Petchey & Gaston 2002; Hooper *et al.* 2005; Lavorel *et al.* 2007).

FD is a component of biodiversity that goes beyond traditional diversity concepts as it relates to the functional interactions of organisms with their environment, rather than the taxonomic richness of communities (Petchey, O'Gorman & Flynn 2009). It can be defined as the range, dispersion, and relative abundance of functional traits of organisms in a given ecosystem (Díaz et al. 2007), where those traits can be any morphological, phenological, or physiological characteristics that can influence the fitness of organisms by affecting their performance (Violle et al. 2007) or govern ecosystem functioning (Jax 2010). Over the last few years, the methodological and theoretical development of FD has advanced considerably (Walker & Langridge 2002; Mason et al. 2005; Petchey & Gaston 2007; Laliberté & Legendre 2010). Current scientific consensus is that FD is comprized of different components, slightly analogous to species diversity: functional richness, functional dispersion, functional evenness, and functional divergence (Mason et al. 2005; Villéger et al. 2008). The different components relate to the spread and distribution of functional traits within communities and are assumed to be independent of each other and, hence, reflect different community properties. Due to this independent, but yet complementary information, Mouillot et al. (2005) and Mason et al. (2005) stressed the need to consider the different components simultaneously to get a more detailed description of functional diversity. However, there is still a lack of empirical studies, and especially of comparisons between the various indices available (but see Mouchet et al. 2010), to understand both drivers and stressors, but also the ecological meaning of the various components of FD (Schleuter et al. 2010). Moreover, many taxonomical groups and habitats are still underrepresented in FD studies, making it difficult to derive general predictions.

Floodplains provide excellent opportunities to analyze the functional relationships between organisms in fluctuating environments, because flood disturbance is a main driving force controlling both the spatial and temporal distribution of organisms (Renofalt *et al.* 2005), as well as their life-history strategies (Lytle & Poff 2004). It is therefore considered to be a key process that affects both the functional and taxonomic attributes of species assemblages in floodplains (Lambeets *et al.* 2008). Surprisingly little is known about functional diversity patterns of terrestrial arthropods under changing environmental conditions. For this study we chose ground beetles as

**CHAPTER FOUR** 70

model organisms because they are one of the most abundant and species-rich taxonomic groups in semi-terrestrial habitats with an important regulative function due to their predatory life form. They further respond strongly to a wide range of environmental factors and are thus exceptionally well-suited for revealing species-environment relationships (Lövei & Sunderland 1996; Rainio & Niemelä 2003).

Here we studied the question how semi-terrestrial ground beetle communities were governed by flood disturbance. Specifically, we evaluated the effects of flood disturbance on different components of functional and species diversity and test whether functional and species diversity react similarly. Because disturbance can enhance the diversity of habitats, species, and their survival strategies, we expected that 1) both species diversity and the richness and dispersion components of functional diversity increased with increasing disturbance intensity. Following disturbances, a few species possessing unique traits-combinations can become extremely dominant (Gerisch et al. 2012). As this would skew the abundance distribution in trait space towards those species, we hypothesized 2) that the components of FD, which consider the abundance weighted distribution and position of traits, decreased with increasing flood disturbance. Although functional approaches try to overcome taxonomic borders, traits are consistently described mostly only on the species level, which is especially true for invertebrates. Yet, it is unclear how the number of species present in a community interacts with their functional diversity. In this study, we aimed to evaluate how species richness affects the different components of FD and to express the ecological meaning of such relationships. Since most of the indices are predicted to reflect independent ecological properties, we expected different effects of species richness on the various FD components.

# Methods

### Study area and survey

We conducted our study in the floodplains of the UNESCO Biosphere Reserve "Elbe River Landscape" in Central Germany. With a length of approx. 1,100 km, the Elbe River is one of the largest rivers in Germany and covers a catchment area of about 150,000 km2 ranging from the German-Czech border to the North Sea near Cuxhaven. Its hydrological regime is close to its natural state and discharge is characterized by high water levels in winter and spring, but low flow in summer (Scholten et al. 2005). We established three distinct study sites within the study area and focus exclusively on seasonally flooded grassland habitats, because this is a representative habitat type of the Biosphere Reserve. The study sites are characterized by typical small-scale relief features, such as permanently and temporary water-filled flood channels and elevated areas with lower flooding frequency and a low groundwater-level (Fig. 1). The more elevated and dryer areas were mown twice a year, whereas the wettest ones (e.g. permanent flood channels) were usually not utilized.

We grouped each of the three study sites into three habitat strata on the basis of vegetation type and site morphology. We placed the same number of sampling plots randomly within each of the three strata, altogether 36 sampling plots on our main study site "Steckby" and 12 sampling plots each in "Wörlitz" and "Sandau". On each sampling plot, we installed five pitfall traps at a distance of 5 m, filled with a 7 % solution of acetic acid and a detergent to reduce surface tension. The traps were exposed for two 14-day periods from April to June and again for

CHAPTER FOUR 71

the same length of time from September to October 2005. We identified all adults at the species level and stored them in a solution of two-thirds ethanol (70 % solution) and one-third acetic acid (60 % solution). See Supplementary material Appendix A1 for a full species list and Henle *et al.* (2006) for a more detailed description of the study design.

### Environmental variables

The environmental characteristics of the sampling plots were intensively studied within the RIVA-project ("Development of a Robust Generally Applicable Indicator System for Ecological Changes in Floodplain Systems") from 1998 to 1999 (Dziock *et al.* 2006). Based on correlations of the RIVA measurements with the Elbe gauge and accounting for evapotranspiration, Follner and Henle (2006) developed a hydrological model that enabled the environmental variables used in this study to be calculated: total flood duration (in weeks), minimum and maximum groundwater depth (in cm), maximum flood height (in meters), number of floods per year, and flood permanency (in weeks) for each plot. Both, the spatial and the temporal transferability of the hydrological model was tested and found appropriate by Follner *et al.* (2010), which ensures that the variables derived from the model are still representative for our study. We quantified all variables from spring 2004, i.e. from the previous year, until the last day of our sampling period in 2005. This time-span sufficiently reflects most of the inter-annual variability without leveling out the differences among the plots too much.

We used an integrative surrogate index for the assessment of flood disturbance. For this, we conducted a centered principal component analysis (PCA) based on the hydrological variables of all sampling plots to ordinate the plots regarding their environmental conditions. We also included the elevation of the sampling plots and the respective land use intensity as a further explanatory variable. We standardized the environmental variables to zero mean and unit variance to equally weight the variables used and to remove the influence of different scale units on the ordination results. We used the ordination scores of the sampling plots along the first axis of the PCA as the disturbance index (DI) and scaled the original plot scores from zero (i.e. low flood disturbance):

$$DI_i = 1 - \frac{x_i - x_{min}}{(x_{max} - x_{min})}$$

with xi being the original ordination score of plot i;  $x_{min}$  being the smallest value of a vector containing all plot scores, and  $x_{max}$  being the highest value of a vector containing all plot scores.

We excluded highly correlated variables (R > 0.75) from the environmental dataset and built the disturbance index based on flood duration (in weeks), water level fluctuation (measured as the variation coefficient of weekly groundwater depth values), the number of floods per year, and land use intensity. The first two axes of the PCA based on the reduced environmental data explained 56.08 % and 25.25 % of the total variance, respectively. Flood duration and water level fluctuation contributed most to the first axis, whereas the other two variables were mostly related to the second axis.
#### Species and functional diversity indices

Prior to the functional diversity analysis, we investigated different components of species diversity for each plot: rarefied species richness, species abundances (standardized by the number of days a trap was active), Pielou's evenness and Simpson's diversity to better understand the response of traditional taxonomic measures to flood disturbance.

Based on the literature, we made an a priori selection of species traits to be used for the calculation of FD. In particular, we selected wing morphology, overwintering strategy, and body size, which are known to be key traits in riparian ground beetles for coping with flood disturbance (Rothenbücher & Schaefer 2006; Lambeets *et al.* 2008). Wing morphology of ground beetles is important for both dispersal and re-colonization ability, and each species was assigned to each of the following categories: macropterous (winged), brachypterous (wingless), and dimorphic (both forms can appear within a species). Adult overwintering is crucial for many species because it enables them to quickly recolonize flooded areas in spring when floods occur regularly. We distinguished between species being adult in spring, autumn, or in both seasons. For invertebrates, small body size is expected to be an indication of a high reproduction rate, which is of great ecological importance for communities inhabiting frequently disturbed habitats (Statzner & Bêche 2010). We used body size as a continuous variable, calculated as the mean between the minimum and maximum value found in the literature. We collated trait information from standard identification keys and ground beetle compendia in a database. See Appendix A1 for the assigned trait values and the references used.

We used various measures that have been recommended in the literature to express the FD of ground beetle communities along a gradient of flood disturbance (Table 1). As probably one of the most intuitional measures, we calculated the degree of functional similarity, which was measured as the amount of species featuring identical trait combinations. Apart from that, we mainly focused on distinguishing between the different components of FD. The richness component of FD reflects the range of the trait values within a multidimensional trait space and can therefore indicate the richness of functional ways in which species interact with their environment (Mason et al. 2005). We calculated it by means of two different indices, which are based on different conceptual and analytical approaches. The FD index of Petchey & Gaston (2002), referred to as FD<sub>P&G</sub> in the following, is a dendrogram based index measuring the total branch length of a functional dendrogram of a community. It represents the functional complementary among species, i.e. the larger the functional differences between species, the larger FD. The multidimensional F<sub>Ric</sub> index of Villéger et al. (2008) measures the amount of functional space filled by a community. It is also known as the convex hull volume, which is defined by the most extreme trait values within a community. As both measures are not independent from species richness, are sensitive to species featuring extreme trait values, and do not integrate species abundances (Podani & Schmera 2006), Laliberté & Legendre (2010) proposed to additionally assess the functional dispersion of a community, which is calculated as the abundance weighted mean of the functional distances of all species to the common centroid of all species. This index, referred to as F<sub>Dis</sub> in the following, is fully independent of species richness and less sensitive to outliers. We further compared another measure for functional dispersion, Rao's quadratic entropy (abbreviated in the following as RaoQ), to these indices. This index is very similar to F<sub>Dis</sub> and is calculated as the product of the distance between a pair of species based on the differences of their traits and the relative abundances of the species (Botta-Dukát 2005). The evenness component of FD identifies whether the resources, i.e. functional niches, are evenly exploited by

the species (Mason *et al.* 2005; Villéger *et al.* 2008). It will be lower if some parts of the filled niche space are densely populated and others only sparsely (Mouchet *et al.* 2010). For the functional evenness component we used the  $F_{Eve}$ -index (Villéger *et al.* 2008), which measures the regularity of the distribution of abundances in multidimensional trait space. To determine how highly abundant species contribute to FD, Villéger *et al.* (2008) proposed to additionally measure functional divergence as the distance of the most abundant species to the centre of gravity in functional trait space. Functional divergence ( $F_{Div}$ ) therefore measures the degree to which the abundance distribution maximizes the spread of functional characters within trait space. For example, adding an abundant species that features traits which are close to the centre of gravity would decrease functional divergence, whereas an abundant species with extreme trait values would increase divergence.

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		al ulversity multes used in this study.		
FD component	Index used	Type of measurement	Abundance weighted	References
Functional richness	FD <sub>P&amp;G</sub>	Total branch length of a functional dendrogram	No	Petchey & Gaston (2002)
	F <sub>Ric</sub>	Convex hull volume (trait space) filled by a community	No	Mason <i>et al.</i> (2005), Villéger <i>et al.</i> (2008)
Functional dispersion	F <sub>Dis</sub>	Mean distance in trait space of individual species to the centroid of all species.	Yes	Laliberté & Legendre (2010)
	RaoQ	Pairwise functional differences between species	Yes	Botta-Dukat (2005)
Functional evenness	F <sub>Eve</sub>	Degree to which abundances are equally distributed in trait space	Yes	Mason <i>et al.</i> (2005), Villéger <i>et al.</i> (2008)
Functional divergence	F <sub>Div</sub>	Degree to which the abundance distribution spreads the distri- bution of functional characters within trait space	Yes	Mason <i>et al.</i> (2005), Villéger <i>et al.</i> (2008)
Degree of functional similarity	% fssp	Amount of species possessing similar combination of functional traits	No	-

Due to the hierarchical structure of our sampling design, we used generalized linear mixed effects models (GLMM, fitted by the Laplace approximation) to test for the effects of flood disturbance on species and functional diversity measures of ground beetle communities. We used the disturbance gradient as fixed effect and defined the hierarchical structure (sampling plots nested within strata and within study sites) as random effect. We tested for the significance of quadratic and logarithmic terms of the fixed effect by means of  $\chi^2$  (tests and by comparing the

log-likelihood and the Akaike information criterion (AIC) of the respective models. We assumed a Poisson error distribution for models with species richness and species abundances as response variables. For the degree of functional similarity, we built the models assuming binomial errors. We set-up all other models with respect to a Gaussian error distribution and evaluated the significance of the fixed effects using Markov chain Monte Carlo sampling with 10,000 permutations. We used the GPL software R (R Development Core Team 2011) for all analyses.

### Results

Altogether we recorded 42,461 individuals from 120 ground beetle species. Sixteen species were trapped with only one specimen and 36 species with less than five specimens (see Appendix A1 for a full species list with abundances standardized by the number of trap-days). Seven species made up almost 50 % of the total ground beetle density, with *Agonum emarginatum* being the most dominant species with 20.8 %, followed by *Poecilus versicolor* (9.0 %), *Carabus granulatus* (7.6 %), *Agonum micans* (6.7 %), *Poecilus cupreus* (5.0 %), *Nebria brevicollis* (4.5 %) and *Pterostichus melanarius* (4.4 %). We found a positive relationship between flood disturbance and ground beetle species richness, evenness, and Simpson's diversity (Fig. 1, Table 2), which were significantly higher on the frequently disturbed plots compared to the more elevated, rarely inundated areas. There was a bell-shaped response of species abundances to flood disturbance, with more individuals occurring at intermediate disturbance levels.





**Table 2** Parameters of GLMMs used to analyze the relationship between species and functional diversity measures and the flood disturbance gradient (DI). ED: Error distribution (P: Poisson, G: Gaussian, B: Binomial), DNull: Null deviance, DRes: Residual deviance, DI<sup>2</sup> and log (DI) indicate significant quadratic and logarithmic effects of the fixed effect, respectively. SE: standard error of parameter estimates, p: p-value of parameter estimates, cor.sp: Spearman rank correlation with the (rarefied) number of species. Significances: \*\*\*: < 0.001, \*\*: < 0.01, \*: < 0.05, n.s.: not significant. For index abbreviations and explanations see Table 1 & Methods section.

Community metrics (explanatory variables)	ED	D <sub>Null</sub>	D <sub>Res</sub>	Estimates	SE	р	cor.sp
Species diversity							
Rarefied species richness	Р	78.18	57.03	DI : - 2.49 log(DI): 4.49	0.86 1.26	** ***	_
Standardized abundances	Р	1101	770.4	DI : 4.29 DI <sup>2</sup> : - 3.35	0.24 0.22	*** ***	n.s.
Pielou's evenness	G	- 125.7	- 142.2	DI:0.52 DI <sup>2</sup> :-0.31	0.16 0.15	*** *	0.90 (***)
Simpson's diversity	G	- 133.6	- 152.0	DI:0.51 DI <sup>2</sup> :-0.30	0.147 0.142	*** *	0.86 (***)
Functional diversity							
FD <sub>P&amp;G</sub>	G	705	678.9	DI : 534.5 DI <sup>2</sup> : - 309.0	137.5 142.0	*** *	0.68 (***)
F <sub>Ric</sub>	G	- 976.7	- 977.1	0	0	0.50	n.s.
F <sub>Dis</sub>	G	- 157.4	- 170.9	-0.19	0.04	***	n.s.
RaoQ	G	- 261.4	- 272.5	- 0.07	0.02	***	n.s.
F <sub>Eve</sub>	G	- 161.4	- 181.3	-0.16	0.03	***	- 0.36 (***)
F <sub>Div</sub>	G	- 127.4	- 152.9	- 0.30	0.05	***	- 0.35 (***)
% fssp	В	106.8	81.8	DI : 7.89 DI <sup>2</sup> : - 5.67	1.87 1.65	***	0.51 (***)

The amount of functional similar species, i.e. those featuring identical trait combinations, significantly increased with increasing disturbance intensity, although we found a significant decrease at the most disturbed plots (Fig. 2, Table 2). FD<sub>P&G</sub> was significantly higher in frequently disturbed plots, whereas  $F_{Ric}$  was the only index that showed no significant relationship to flood disturbance. In contrast, the functional dispersion measures  $F_{Dis}$  and RaoQ, as well as functional evenness  $F_{Eve}$ , and functional divergence  $F_{Div}$  decreased significantly with increasing flood disturbance (Fig. 3, Table 2). The degree of correlation between (rarefied) species richness and the different components of FD was inconsistent: it was intermediate for  $FD_{P&G}$  and for the amount of functional similar species but not significant for  $F_{Ric}$  and for the dispersion component of FD ( $F_{Dis}$  and RaoQ). In contrast, both  $F_{Eve}$  and  $F_{Div}$  were slightly negatively correlated with (rarefied) species richness (Table 2).

More species, but all do the same – Contrasting effects of ground beetle species and functional diversity to flood disturbance



**Figure 2** Relationships between flood disturbance (DI) the degree of functional similarity, and the richness component ( $FD_{P&G}$  and  $F_{Ric}$ ) of ground beetle functional diversity. The solid lines represent model predictions based on GLMMs. For index abbreviations and explanations see Table 1 and Methods. \*\*\*: p < 0.001, n.s.: not significant.



**Figure 3** Relationships between flood disturbance (DI) and the dispersion ( $F_{Dis}$  and RaoQ), evenness ( $F_{Eve}$ ), and divergence ( $F_{Div}$ ) components of FD of floodplain ground beetles. The solid lines represent model predictions based on GLMMs. For index abbreviations and explanations see Table 1 and Methods. \*\*\*: p < 0.001.

More species, but all do the same – Contrasting effects of ground beetle species and functional diversity to flood disturbance

### Discussion

### Enhanced species diversity from flood disturbance

Most species diversity measures used in this study increased significantly with increasing flood disturbance intensity, except species abundances, which showed a hump-shaped relationship, with highest numbers on medium disturbed plots. The strong and fostering effects of flood disturbance on species diversity assumes higher resource diversity in frequently flooded habitats, because many riparian ground beetles predate on (semi-) aquatic insects that emerge ashore, such as stoneflies or collembolans (Paetzold, Bernet & Tockner 2006). This outcome only partly supports predictions derived from prominent disturbance related hypotheses, such as the intermediate disturbance hypothesis (IDH, Connell 1978) or the stress hypothesis (SH, Grav 1989). Whereas the IDH predicts the highest species diversity at intermediate disturbance levels, the SH implies a decrease in diversity with increasing disturbance. Consequently, both theories imply that species diversity will decrease in highly disturbed habitats, which we can also support here. We found clear evidence that species abundances decreased at the right-hand side of the disturbance gradient. Furthermore, we observed saturated curves or slight decreases, respectively, for all other species diversity indices at highest disturbance intensities (Fig. 1). Hence, species diversity in this study is significantly fostered by disturbance, which clearly contradicts the SH. On the other hand, further increasing disturbance intensities would mean a decrease in species diversity, which supports both the IDH and the SH. There are also supporting and contradicting results for both theories recorded in the literature and it is still not fully understood whether the response of biodiversity can be described by general rules (Cadotte 2007). This is also true for a number of ground beetle studies, including this one. For example, Magura, Tóthmérész & Molnár (2004) found increasing ground beetle diversity along urbanization gradients that were related to different disturbance regimes. Cárdenas & Buddle (2008) reported highest species richness of ground beetles with increasing land use intensity. A possible reason for inconsistencies between theory and empiricism is the difficulty or even impossibility of matching environmental gradients to the ecological response scale of a particular species group. In many cases, the effective disturbance gradient is too short, which often leads to response patterns seemingly contradicting existing theories. We realize that this could also be partly true for our study, because we did not survey frequently flooded riverbanks and rarely flooded areas on elevated ridges and therefore the extreme ends of the disturbance gradient are underrepresented.

#### Flood disturbance effects on functional diversity

Trait-based approaches, such as FD, can help identifying mechanistic relationships between environmental variability and the response of biodiversity (Hooper *et al.* 2005). Ours is one of the first empirical studies that measure the different components of FD of a terrestrial invertebrate system in response to habitat disturbance. We found that flood disturbance is an important driver not only for traditional species diversity measures, but also for the functional diversity of floodplain ground beetles.

The amount of ground beetle species being functionally similar and the  $FD_{P\&G}$  index increased significantly with increasing flood disturbance. This supports recent trait-based hypotheses claiming that disturbance acts as a filter, sorting survival strategies of the species so that only species can pass through these filters, whose functional traits match the specific environment (Poff 1997). Surprisingly, while these two measures of functional richness increased with flood disturbance, functional dispersion components  $F_{Dis}$  and RaoQ decreased with disturbance.

More species, but all do the same – Contrasting effects of ground beetle species and functional diversity to flood disturbance

This could be explained by only specific trait combinations remaining suitable to cope with rapidly increasing disturbance intensities. Previous work already showed that body size, overwintering strategy, and wing morphology are critical for alluvial ground beetles to cope with floodplain dynamics (Rothenbücher & Schaefer 2006; Lambeets et al. 2008). These traits can serve as proxies for high mobility and rapid development and thus favour species colonization and population recovery after flood events. Consequently, only successful trait combinations pre-adapt species to environmental stressors, i.e. flood disturbance, which resulted in relatively little functional differences between the species on highly disturbed sites. Besides the dispersion of functional characteristics, also functional evenness decreased with increasing disturbance levels, which contrasts to the increasing species evenness along the same flood disturbance gradient. Villéger et al. (2008) noted that both components, species evenness and functional evenness, are closely connected: either functional evenness decreases when abundances are less evenly distributed among the species or when the abundance weighted functional distances among species are less regular. Because the first is not the case in our study (see results for Pielou's evenness), we infer that few abundant, functional different species, such as Poecilus versicolor or Pterostichus melanarius, caused this skewed abundance distribution in trait space and therefore decreasing F<sub>Eve</sub> values with increasing disturbance. Contrary to our study, Filippi-Codaccioni, Globert & Julliard (2009) found functional evenness of avian communities increasing with urbanization and they explained this pattern with a decrease of specialist species in urban areas. Also Devictor et al. (2008) found specialist species being more affected by habitat disturbance than generalist species. We assume similar in our study because some highly abundant species in frequently disturbed habitats display trait combinations that differ from the centre of gravity (the average functional trait composition). For example, the former two species are generalist species, occurring in a wide range of different habitats and therefore feature different survival strategies compared to typical floodplain specialists. We therefore believe that in this study functional evenness indicates the degree of how abundant, functionally different species invaded communities. Mason et al. (2005) argued that low functional evenness could also relate to an underutilisation of particular functional niches occupied by a community, because some abundant species exploit specific resources through their high abundance. However, this is only valid if available niches are evenly distributed and this might not be the case in highly dynamic floodplain systems comprized of a diverse mosaic of different habitats.

As demonstrated in this study, also Villéger *et al.* (2010) found decreasing F<sub>Div</sub> of fish species facing severe environmental changes, which generally supports our results. Garrett *et al.* (2009) found lower functional divergence in host plants and explained this by lower differences in resistance types to plant diseases. The decreasing functional divergence observed here indicates that, although total species richness increased and generalists skewed the abundance distribution in trait space, most of the species use the same mainstream life history strategies to cope with flood disturbance. This may complement the predictions of functional dispersion, but due to the low number of studies that empirically assessed the different FD components, it not fully clear to which degree functional dispersion, evenness, and divergence explain similar or different ecological attributes of communities.

More species, but all do the same – Contrasting effects of ground beetle species and functional diversity to flood disturbance

#### Relationships between species richness and functional diversity

In this study, the correlation between (rarefied) species richness and FD depended on the index used. Correlations were high for the richness measures of FD but low for the functional evenness, dispersion, and divergence measures. Bihn, Gebauer & Brandl (2010) similarly found a strong and positive correlation between species and the functional richness of tropical leaf litter ants and Petchey et al. (2007) reported similar observations for avian communities along temporal trajectories. They related this to a low functional redundancy, i.e. the degree to which species perform similar ecological functions. Following their argumentation, the relationship between species richness and the degree of functional similarity found in our study would indicate increasing functional redundancy with increasing flood disturbance. Species inhabiting the most flood disturbed habitats perform similar functional roles, because there are only a few species that are functionally different from the centre of gravity when flood disturbance is high (low F<sub>Div</sub> and F<sub>Dis</sub> values). We thus assume that under high disturbance levels, the loss of a species would not have a serious impact on the functioning of the community (e.g. regarding resilience), because there are several species present that are performing similar functional roles. This theory, however, is only valid if species extinct independent of their evolved traits (which is not always the case: see Schweiger et al. 2007). For example, if rapidly altered environmental conditions do not match historically-evolved adaptations (e.g. in the course of extreme events), the probability is high that functionally unique species would be affected in a similar way and that high functional redundancy would not contribute to flood resistance of the community. There is some empirical evidence for the latter, because Gerisch (2012) found low resilience capacity of highly flood adapted ground beetle communities following an extreme, unpredictable flood event.

#### Conclusions

In this study we assessed how the different components of functional and species diversity are governed by flood disturbance. Generally, we confirmed other studies showing that habitat disturbance is a main driver not only for species diversity, but also for the distribution of functional characteristics within communities. We further identified a rarely observed inverse relationship between flood disturbance, species diversity, and functional diversity: while species diversity components increased, functional dispersion, evenness, and divergence measures significantly decreased at high disturbance levels. Our results suggest that trait filtering mechanisms lead to a higher functional similarity of species inhabiting frequently disturbed plots. The co-occurrence of a high number of species could be explained by combined effects of functional redundancy and unequal resource exploitation, but also stochastic immigration effects can govern FD, which however are difficult to eliminate. On the one hand we show that the assessment of species diversity and functional diversity can complement each other and contribute to a better understanding of the ecological effects of disturbance. One the other hand, more empirical studies are needed to recognize their role for a general understanding of ecological patterns and processes.

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## Appendices

**Appendix A1** 1/5 Full species list representing the standardized number of individuals per species for the study sites Steckby, Woerlitz, and Sandau. Density expresses the proportion of species standardized abundances to total abundance. Macropterous = winged, brachypterous = wingless, dimorphic = both forms can appear with a species. Body size is the average of maximum and minimum values found in the literature (for references see below).

Species	Steckby	Woerlitz	Sandau	Density	Wing Morphology	Repro- duction Season	Body size in mm
Acupalpus dubius	0.032	0	0.016	0	macropterous	spring	2.6
Acupalpus exiguus	1.838	1.019	0.71	0.005	macropterous	spring	2.7
Acupalpus parvulus	0.081	0.038	0.032	0	macropterous	spring	3.6
Agonum dolens	0.032	0.038	0.081	0	dimorph	spring	8.8
Agonum duftschmidi	14.966	2.755	0.016	0.025	macropterous	spring	8.2
Agonum emarginatum	116.659	4.472	25.194	0.208	macropterous	spring	7.2
Agonum fuliginosum	0.097	0.038	0	0	dimorph	spring	6.7
Agonum lugens	0.177	0	0.081	0	macropterous	spring	9
Agonum marginatum	0.371	0.075	0.113	0.001	macropterous	spring	9.2
Agonum micans	19.502	4.208	23.71	0.067	macropterous	spring	6.6
Agonum muelleri	0	0.019	0	0	macropterous	spring	8.2
Agonum piceum	0.468	0	0.016	0.001	macropterous	spring	6.4
Agonum sexpunctatum	0.032	0	0.061	0	macropterous	spring	8.2
Agonum thoreyi	0.016	0	0	0	macropterous	spring	6.8
Agonum versutum	6.016	1.887	0.097	0.011	macropterous	spring	7.5
Amara aenea	0.15	0.057	0.161	0.001	macropterous	spring	7.5
Amara aulica	0.065	0.887	0.048	0.001	macropterous	autumn	12.6
Amara bifrons	0.016	0.057	0.016	0	macropterous	autumn	6.3
Amara communis	3.657	0.302	1.065	0.007	macropterous	spring	6.8
Amara convexior	0	0	0.016	0	macropterous	spring	7.8
Amara equestris	0.661	0.358	0	0.001	macropterous	autumn	10.9
Amara familiaris	0.231	0.113	0.145	0.001	macropterous	spring	6.5
Amara lunicollis	1.73	0.094	0.048	0.003	macropterous	spring	7.7
Amara ovata	0.15	0.038	0.032	0	macropterous	spring	8.6
Amara plebeja	0.231	0.019	0.065	0	macropterous	spring	7
Amara similata	0.145	0.226	0.065	0.001	macropterous	spring	8.8
Amara spreta	0	0	0.032	0	macropterous	spring	8

Appendix A1 2/5							
Species	Steckby	Woerlitz	Sandau	Density	Wing Morphology	Repro- duction Season	Body size in mm
Amara strenua	1.42	0.038	0.032	0.002	macropterous	spring	9
Amara tibialis	0.048	0.019	0.048	0	macropterous	spring	5
Anchomenus dorsalis	0	0	0.048	0	macropterous	spring	6.7
Anisodactylus binotatus	6.896	3	0.935	0.015	macropterous	spring	11
Anthracus consputus	3.995	0.34	0.226	0.006	macropterous	spring	4.5
Badister bullatus	0.021	0	0	0	macropterous	spring	5.5
Badister meridionalis	0.048	0.038	0.016	0	macropterous	spring	6.7
Badister sodalis	0.102	0	0	0	dimorph	spring	4.2
Badister unipustulatus	0.129	0.019	0.016	0	macropterous	spring	7.9
Bembidion argenteolum	0.016	0	0	0	macropterous	spring	6.5
Bembidion assimile	0.371	0	0.113	0.001	dimorph	spring	3.2
Bembidion biguttatum	8.279	2.415	4.306	0.021	macropterous	spring	4
Bembidion bruxellense	0	0.019	0	0	macropterous	spring	4.7
Bembidion dentellum	6.88	5.623	5.468	0.026	macropterous	spring	5.5
Bembidion fumigatum	0.048	0	0	0	macropterous	spring	3.8
Bembidion gilvipes	0.626	0.132	0.161	0.001	dimorph	spring	2.8
Bembidion guttula	5.715	0.83	1.419	0.011	dimorph	spring	3.3
Bembidion lampros	0	0.113	0	0	dimorph	spring	3.6
Bembidion lunulatum	0.065	0.038	0	0	macropterous	spring	3.7
Bembidion minimum	0.016	0	0.016	0	macropterous	spring	2.8
Bembidion obtusum	0	0	0.016	0	dimorph	spring	3
Bembidion octomaculatum	0.032	0	0	0	macropterous	spring	2.5
Bembidion properans	0.032	0.113	0.177	0	dimorph	spring	4
Bembidion quadrimaculatum	0.032	0.038	0	0	macropterous	spring	3
Bembidion semipunctatum	0.065	0.283	0.968	0.002	macropterous	spring	3.8
Bembidion tetracolum	0.032	0.226	0.452	0.001	dimorph	spring	5.3
Bembidion varium	0.016	0	0.032	0	macropterous	spring	4.3
Blethisa multipunctata	0.226	0	0.038	0	macropterous	spring	11.8

Appendix A1 3/5							
Species	Steckby	Woerlitz	Sandau	Density	Wing Morphology	Repro- duction Season	Body size in mm
Bradycellus harpalinus	0.016	0	0	0	dimorph	spring	4.3
Calathus fuscipes	1.505	0.396	0	0.003	dimorph	autumn	11.8
Calathus melanocephalus	0.71	0.151	0.032	0.001	dimorph	autumn	7.5
Carabus auratus	0.032	0	0	0	brachypterous	spring/ autumn	23.5
Carabus glabratus	0.194	0	0	0	brachypterous	spring	28
Carabus granulatus	34.288	8.528	10.839	0.076	brachypterous	spring	19.5
Carabus nemoralis	0.048	0.283	0.016	0	brachypterous	spring	23
Chlaenius nigricornis	8.405	1.943	3.016	0.019	macropterous	spring	11
Chlaenius tristis	0.016	0	0	0	macropterous	spring	11.8
Clivina collaris	0	0	0.016	0	macropterous	spring	5.3
Clivina fossor	12.561	7.962	10.5	0.044	dimorph	spring	6
Cychrus caraboides	0.016	0	0	0	dimorph	autumn	16
Demetrias monostigma	0.081	0	0	0	dimorph	spring	4.5
Dyschirius aeneus	0.065	0.057	0.032	0	macropterous	spring	3.1
Dyschirius globosus	0.481	0.057	0.097	0.001	dimorph	spring	2.5
Dyschirius luedersi	0.258	0.057	0.081	0.001	macropterous	spring	3.6
Dyschirius politus	0	0	0.016	0	macropterous	spring	4.3
Elaphrus cupreus	0.548	0.019	0.452	0.001	macropterous	spring	2
Elaphrus riparius	0.161	0.057	0.323	0.001	macropterous	spring	6.8
Epaphius secalis	0.684	0.151	0.065	0.001	brachypterous	autumn	3.6
Harpalus affinis	0	0.208	0.048	0	macropterous	spring/ autumn	10.2
Harpalus distinguendus	0.032	0	0	0	macropterous	spring/ autumn	9.6
Harpalus latus	0.456	0.717	1.435	0.004	macropterous	spring/ autumn	9.5
Harpalus luteicornis	0.194	0.245	0.276	0.001	macropterous	spring/ autumn	7
Harpalus signaticornis	0.037	0	0	0	macropterous	spring	6.8
Loricera pilicornis	10.284	0.981	12.71	0.034	macropterous	spring	7.3

Appendix A1 4/5							
Species	Steckby	Woerlitz	Sandau	Density	Wing Morphology	Repro- duction Season	Body size in mm
Microlestes minutulus	0.016	0.113	0	0	dimorph	spring	3.2
Nebria brevicollis	27.497	4.057	0.016	0.045	macropterous	autumn	12
Notiophilus aquaticus	0.016	0	0	0	dimorph	autumn	5.1
Notiophilus palustris	0.048	0	0	0	dimorph	spring	5
Odacantha melanura	0.016	0	0	0	macropterous	spring	6.8
Omophron limbatum	0.016	0	0.048	0	macropterous	spring	5.5
Oodes helopioides	5.713	0.208	0.129	0.009	macropterous	spring	8.5
Ophonus diffinis	0	0.075	0	0	macropterous	spring	11.2
Ophonus rufibarbis	0	1.283	0	0.002	macropterous	spring	7.8
Oxypselaphus obscurus	1.181	0	0.016	0.002	dimorph	spring/ autumn	5.5
Patrobus atrorufus	0.788	0.981	0	0.003	brachypterous	autumn	8.5
Philorhizus sigma	0.065	0.019	0.032	0	dimorph	spring	3.2
Platynus assimilis	0.306	2.66	0.661	0.005	macropterous	spring	10.5
Platynus livens	0.097	0.189	0	0	macropterous	spring	9
Platynus longiventris	0.016	0	0	0	macropterous	spring	13
Poecilus cupreus	7.002	7.792	20.113	0.05	macropterous	spring	11.5
Poecilus versicolor	53.799	6.566	2.935	0.09	macropterous	spring	10.1
Pseudoophonus griseus	0	0.038	0	0	macropterous	autumn	10.1
Pseudoophonus rufipes	0.355	5.868	1.435	0.011	macropterous	spring/ autumn	13.3
Pterostichus anthracinus	11.932	2.962	3.887	0.027	dimorph	spring	11.2
Pterostichus diligens	0.081	0	0.032	0	dimorph	spring	5.6
Pterostichus gracilis	8.725	0.585	2.694	0.017	macropterous	spring	9
Pterostichus melanarius	11.043	19.623	0.597	0.044	dimorph	autumn	15.3
Pterostichus minor	0.177	0.019	0.016	0	dimorph	spring	7.3
Pterostichus niger	0.272	0.264	0.032	0.001	dimorph	autumn	18.3
Pterostichus nigrita	7.861	0.774	4	0.018	dimorph	spring	10.8
Pterostichus oblongopunctatus	0	0	0.016	0	macropterous	spring	11

Appendix A1 4/5

Appendix A1 5/5							
Species	Steckby	Woerlitz	Sandau	Density	Wing Morphology	Repro- duction Season	Body size in mm
Pterostichus rhaeticus	0.032	0	0	0	dimorph	spring	9.7
Pterostichus strenuus	3.536	2.396	2.21	0.012	dimorph	spring	6.1
Pterostichus vernalis	1.762	0.396	2.016	0.006	dimorph	spring	6.8
Stenolophus mixtus	6.452	5.925	2.806	0.022	macropterous	spring	5.7
Stenolophus skrimshiranus	1.339	0.057	0	0.002	macropterous	spring	6.1
Stomis pumicatus	0.016	0.17	0	0	brachypterous	spring	7.5
Syntomus truncatellus	0.101	0	0.032	0	dimorph	spring	2.9
Tachys bistriatus	0.226	0.057	0.016	0	macropterous	spring	2.1
Trechoblemus micros	0.016	0.019	0	0	macropterous	spring	4.3
Trechus obtusus	0.226	0.057	0.016	0	dimorph	autumn	3.8
Trechus quadristriatus	4.583	3.623	5.242	0.019	macropterous	autumn	3.5
Trichocellus placidus	0.032	0	0	0	macropterous	autumn	4.8

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### CHAPTER FIVE Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood

### Abstract

Extreme environmental events are predicted to occur more frequently, but there is scant understanding of the mechanisms that enable biodiversity to re-establish following severe disturbances. Theory predicts species performing similar roles for ecological processes or functions, can compensate for the loss of others and, therefore, functional redundancy (FR) is assumed to promote ecological stability. However, there is no clear evidence for this mechanism, because FR has been observed to be low in many ecological systems. Here I test whether FR exists in floodplain ground beetle communities. I used a severe flood event to examine whether functionally equivalent species can provide "ecological insurance" against, and high resilience to, extreme disturbances. Ground beetles were sampled between 2002 and 2005 in floodplain grassland habitats surrounding the Elbe River, Germany. FR was estimated as the average amount of species in a community that have neutral effects on functional diversity. Null models were used to determine whether FR is higher or lower than expected and mixed effects modelling was applied to estimate the relationships between FR and potential drivers. FR was present in ground beetle communities, but it was, to a considerable degree, random. In most communities it was lowest immediately after the flood and quickly increased to its maximum. I found significantly different FR levels in habitats differentially exposed to flood disturbance. Under certain conditions, FR can promote community stability by providing "insurance" against the loss of functioning. I outline that FR cannot be the only stabilizing mechanism. Especially after extreme events, FR might not be capable of maintaining community functioning, because all species are similarly exposed and usually cannot cope with such extremes. Other regulating forces, such as stochastic immigration processes and the re-developing habitat templet may play more important roles for overall community recovery under such conditions.

**Keywords**: assemblages, biodiversity recovery, carabids, ecosystem functioning, species turnover, stochastic events, traits

I affirm that I am the sole author of this chapter. I developed the idea, performed all analysis and wrote the whole chapter. This part of the dissertation is not submitted, considered for publication, or published elsewhere.

This chapter is intended for publication as

Gerisch, M Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood in Journal of Animal Ecology.

## Introduction

Extreme events, such as catastrophic floods, droughts, or fires, have serious implications for ecosystems (Easterling et al. 2000; Jentsch et al. 2007). They can cause sudden declines of species and communities (Thibault & Brown 2008), change competitive interactions between organisms (Jentsch & Beierkuhnlein 2003), or even shift ecotone boundaries (Allen & Breshears 1998). Hence, one of the prime effects of unexpected weather extremes is that they can abruptly and persistently change the performance of ecological processes, such as biomass production (Ciais et al. 2005), or properties realized by single species or species communities, for example resistance to invasive species (Sorte, Fuller & Bracken 2010). Changes in the functioning of ecological systems, particularly after extreme events, often go along with massive compositional and functional changes in communities (e.g. Mueller et al. 2005; Cardoso et al. 2008). However, there is also evidence that ecological complexity, i.e. the richness of organisms and survival strategies, can buffer against the effects of extreme events and that compositional changes to communities can serve to maintain ecological processes or properties of the entire system (White et al. 2000; Jentsch et al. 2011). Hence, guestions regarding how species gain and species loss affect the functioning of ecological systems following disturbances increasingly stimulate ecological debate (Díaz & Cabido 2001; Naeem & Wright 2003), particularly since the frequency and magnitude of extreme weather events are predicted to increase in the future, while biodiversity effects of extreme events are still poorly understood.

A central theme within these discussions is still basic in nature and encompasses the understanding of the relationships between the number of species present in a community and the performance of ecological processes or properties (i.e. functioning). Functional redundancy (FR) is one potential concept used to predict the effects of species richness on ecosystem functioning, particularly after disturbances (for other such hypotheses see Naeem et al. 2002; Hubbell 2006). FR is based on the principal that some species perform similar functional roles in ecological systems, and might therefore be substitutable with little impact on ecosystem functions, e.g. biomass productivity or nutrient fluxes, or community properties, such as resilience following disturbances (Walker 1992; Lawton & Brown 1993; Rosenfeld 2002). In recent years, the number of studies that focus explicitly on resilience-redundancy relationships has increased for numerous different ecological systems (Micheli & Halpern 2005; Petchey et al. 2007; Bêche & Statzner 2009; Sasaki et al. 2009; Bihn et al. 2010; Joner et al. 2011; Guillemont et al. 2011). Nevertheless, no general picture can be drawn from this work, because FR differs considerably among habitats, taxonomic groups, and functional units, but also in response to various types of environmental stressors and disturbance agents. A common finding of most of the studies is the low degree of FR detected (but see Villéger et al. 2010), which also implies that some aspects of resilience might be lower than expected in many ecological systems. In fact, FR and specific facets of resilience are closely connected (Naeem et al. 2002; Petchey & Gaston 2009; Konopka 2009; Dalerum et al. 2010). This is most obvious for functional resilience, which is the capacity of a community to buffer disturbances without changing its ecological functioning (Walker 1992). In this context, if I assume species losses to be a disturbance for community functioning and functional diversity (FD, i.e. the range, dispersion, and relative abundance of functional traits of organisms in a given ecosystem, Díaz et al. 2007) to be a measure of ecological functioning, then functional resilience can be viewed as the capacity of a community to maintain its FD if species get lost from the system (Petchey & Gaston 2009; Dalerum et al. 2010). In such a functional view of resilience, communities are considered to be highly resilient

CHAPTER FIVE 90 Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood

if many species can get lost without changing the FD. Functional resilience is therefore assumed to explain different parts of community reorganization from taxonomic approaches, which usually estimate taxonomic dissimilarities to some reference conditions, i.e. beta-diversity (Moretti *et al.* 2009). But, particularly in the course of extreme events, communities are not only affected by massive species turnover rates, but also by severe changes in functional composition due to the taxonomic changes.

In the summer of 2002, unpredictable severe precipitation led to the highest flooding ever recorded along the river Elbe in Germany. This flood was extreme in terms of its height, duration, and seasonal and spatial occurrence (Schiermeier 2003). In a previous study, Gerisch et al. (2012) showed a rapid recovery of ground beetle species richness and diversity after being massively reduced by this extreme summer flood. The present study builds upon this work and aims to obtain a better understanding of how quickly and effectively communities can functionally recover from such extreme floods, and what role is played by FR in community re-organization. The major aim is to determine whether FR is present in species communities in fluctuating environments, identify potential drivers of FR, and test whether functionally redundant species can provide "insurance" (see Yachi & Loreau 1999) against, and high resilience to, extreme disturbances. I focus on ground beetles in floodplain grasslands because they are one of the most abundant macroinvertebrate groups. They are also known to respond quickly and differentially to habitat disturbances (Ribera et al. 2001; Niemelä & Kotze 2009). Moreover, functional traits and ecological preferences are widely known for these species. I hypothesized that ground beetle FR in floodplain grassland is higher than would be expected by chance, as this should ensure that species losses would only have little impact on functional diversity and thus allow for a high functional resilience. Following the insurance hypothesis, I also assumed that FR is higher in habitats that are frequently flooded than in sites that are rarely disturbed by flood. Because species were massively reduced in the course of the extreme flood, I also expected a significantly lower FR immediately after the flood, but a guick recovery of functional resilience in subsequent years.

Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood

### **Material and Methods**

#### Data sampling

Ground beetles were sampled at two study sites at the Elbe River in Central Germany. 48 sampling plots were established in seasonally flooded grassland habitats, with 36 plots at the main study site "Steckby," and 12 plots at the site "Wörlitz". Following a stratified randomized sampling design, each site was divided into 3 strata in terms of terrain morphology and vegetation type. The sampling plots were then randomly located within each of the strata, which represent different habitat types: (1) wet grasslands, representing frequently flooded oxbow channels, (2) moist grasslands, representing habitats in intermediate conditions, and (3) fresh grassland, representing elevated, rarely flooded habitats. All plots and all habitats were flooded for several weeks in August 2002, but differ considerably in hydrological conditions during normal years. See Henle *et al.* (2006) for a detailed description of the study design and (Gerisch *et al.* 2012) for a hydrological description of the different habitat types.

On each plot, 5 pitfall traps were installed and filled with a 7 % solution of acetic acid and a detergent to reduce surface tension. By means of an RTK differential GPS, the traps were placed on exactly the same location in each sampling period. The traps were retrieved biweekly from May to June (spring period) and from September to October (autumn period), respectively, between 2002 and 2005. Sampling in the flood year 2002 was carried out only in autumn, as soon as the floodwater had receded. Owing to accidental loss of some traps through wild boars and flooding, species abundances were standardized by the number of functioning trap-days. All adult ground beetles were identified to the species level and we considered all recorded species of a study plot sampled in a particular season as a community.

I collected species traits that are known to control community resilience and which allow for quick re-colonization of ground beetles after flood disturbance (functional effect traits, see Table 1). In addition, I also considered certain traits that are not necessarily related to disturbance, but that illustrate important survival and response strategies to environmental variability and that enable species with similar effect traits to exploit different ecological niches (functional response traits, see Table 1). Effect and response traits were not weighted a priori for their importance, to avoid an overemphasis of certain traits for ground beetle functioning. Traits were collected from standard identification keys and ground beetle compendia (see Appendix A2).

**Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood** 

 Table 1
 Species traits used to calculate functional diversity and redundancy.

Type of functional trait	Trait	Trait categories	Relevance/ecological meaning	No. of species
Effect traits	Wing mor- phology	Macropterous	High dispersal capacity, i.e. high recolonization potential	105
		Brachypterous	Low dispersal capacity, i.e. low recolonization potential	11
		Dimorphic	Intermediate dispersal capacity	37
	Mode of overwintering	Adult	Is correlated with time of activity, but seems to the better predictor. Species emerge as adults in early spring and can therefore quickly recolonize flooded areas.	113
		Larvae	Species emerge as adults in late summer or autumn.	22
		Both	Species can reproduce either in spring or autumn. Possibly dependent on habitat or geographical locality.	18
	Body size	Continuouse	One of the most important traits shaping species physiology and life-history.	153
Response	Feeding mode	Carnivorous	Species can co-occur in the same	93
traits		Phytophagous	strategy.	23
		Polyphagous		36
	Daily activity	Diurnal	Species can co-occur in the same	69
		Nocturnal	separated temporal niches.	75
		Both		9
	Light	Unshaded	Species can co-occur in the same	92
	preference	Partly shaded	for micro habitats.	37
		Mainly shaded		24
	Humidity	Hygrophilus	Important preference trait in wetlands	96
	preference	Mesophilous	for niche separation.	21
		Xerophious		36
	Habitat	Eurytopic	Generalist species are often the first	106
	specialization	Stenotopic	arrivals after disturbances.	47

Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood

### Measuring functional diversity and functional redundancy

FR in this study was measured as the change in FD caused by the addition of a species, and a species was considered functionally redundant if its arrival did not increase community FD further. Because FD depends on which species are added to or removed from a community, functional bootstrapping was applied on subsets of species by repeatedly measuring the FD of different species combinations. For each community, 2 to *i* species were randomly selected from its species pool, where 2 is the minimum number of species needed to calculate FD, and *i* is the total number of species of the community. As a result, i-1 different species combinations were obtained, which I refer to as species subsets for the remainder of this paper. Gower dissimilarity was then calculated between the species of each species subset based on the selected functional traits. FD was estimated by means of the functional dispersion index, which is the mean distance of individual species from the centroid of all species in multivariate trait space (Laliberté & Legendre 2010). Functional dispersion indicates how strongly species are spread in this multidimensional space. Large values reflect a large distance between the species in the trait space, meaning that several species possess traits that differ from the multivariate average. Our simulation revealed that the average functional dispersion of a species subset can be higher than the observed functional dispersion of the source community. This was sometimes the case in species-poor subsets, with 1 species being extremely abundant. Obviously, certain combinations of species traits and abundances can increase the average distances between species in a trait space and lead to higher functional dispersion values compared with the full species set. As this can bias the degree of FR, I standardized the FD of each species subset by dividing it by the maximum FD that can possibly be reached by this subset. As a result, the standardized FD varies between 0 and 1, where 1 means that the species subset possesses the highest FD possible, and decreasing values refer to increasing FD losses of a subset compared with the maximum FD.

This step of calculating standardized FD values was repeated 1,000 times for each subset size between 2 and *i* to obtain a data matrix with columns corresponding to the size of the species subset (number of columns = i-1), rows corresponding to the number of replications (number of rows = 1,000), and cells containing the standardized FD values. The means of each column were calculated, which represent the average difference of a subset's FD from the maximum FD. FR was then estimated as the amount of species that have neutral effects on the FD of a community. That is, identifying the position along the x-axis from where the standardized FD values did not increase further (see Figure 1 for the conceptual approach to calculating FR in this study).

Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood



**Figure 1** Conceptual approach to calculating functional redundancy (FR) in this study. The basis is a speciesby-site matrix with abundances within cells and another matrix containing the traits of each species. Initially, the total number of species/plot (i) was calculated and then 2 to i species were randomly combined into a species subset and a corresponding trait subset. This step was repeated 1,000 times, resulting in 1,000 random species– trait combinations for each subset size. For each pair of species and trait subsets and for each replication step, FD was calculated, standardized (see text) and stored in a matrix (rows = number of replication, columns = subset size). For all subset sizes, the mean standardized FD among the replications was then calculated and FR estimated as the amount of species that did not increase the average FD of a community.

Following a null model approach, I tested whether the observed FR differed from the FR of random species observations. Null models produce community patterns that can be expected when particular ecological mechanisms would not operate and are therefore suitable for detecting

Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood

environmental impacts on ecological properties (Gotelli & Graves 1996). The underlying null hypothesis assumes that species occurrences are not constrained by external driving factors and, hence, that species assemble randomly. To test the alternative hypothesis (that the observed FR values differ from a random distribution), 999 artificial communities were generated for each sampling plot. Permutation was carried out by randomly re-assigning species from the total species pool (which is the full set of species recorded during the study) to the sampling plots. The FR of the artificial communities (n = 999) was calculated for each of the 48 plots as described above. To estimate whether the observed FR is higher or lower than a random observation, the probability (*P*) was calculated that a simulated FR-value of the null distribution takes a value of the observed FR-value or smaller. The opposite case, which is the probability of picking a simulated value that is equal to or larger than the observed value, was calculated as 1 - P. All random FR values followed a normal distribution, and hence *P* was calculated using the function "pnorm" in R. I used  $P \le 0.05$  as a threshold to determine whether the observed FR values were significantly smaller or significantly larger than a random observation. This was repeated for all sampling periods.

#### Fitting mixed effects models

In addition to estimating the extent of FR, a further aim of the study was to test how guickly FR recovered from an extreme flood and how it is related to other potential drivers, such as habitat type. I also related FR to the total number of species and the number of redundant species, respectively, to estimate how different measures of species richness influence the amount of redundant species. Owing to the hierarchical character of the study design, mixed effects models were applied, with sampling plots treated as random effects, because they were repeatedly surveyed over subsequent periods. Model residuals were considerably temporally autocorrelated, tending to be higher within similar seasons (e.g. spring vs. spring periods) than between seasons (e.g. spring vs. autumn periods). To account for this, an auto-regressive moving average (ARMA) process of second order was added to the models, which in all cases improved the models significantly. In cases heteroscedasticity of within-group errors has occurred, the variance was modelled using a constant variance function. To decide whether to fit linear or nonlinear models, the log-likelihood of a non-linear model was compared with its linear variant. The effects of both total number of species and habitat type on FR were modelled by means of a linear mixed effects model. Because of considerably lower log-likelihoods for the linear variants, non-linear modelling was applied for the variables "time after flood" and "number of redundant species". Both non-linear models were set up using a standard Monod equation with the form:

$$\mu = \frac{V_m * x}{(K_m * x)}$$

Where  $\mu$  is the growth rate of FR and x represents the explanatory variable. V<sub>m</sub> is the saturation point, i.e. the maximum value of FR recorded, and K<sub>m</sub> represents the value of x at which FR is half of V<sub>m</sub>.

All analyses were carried out using R (R Development Core Team 2011) and the packages FD, nlme and vegan.

### Results

A total of 153 ground beetle species were sampled during the 7 sampling periods. Five species (*Agonum emarginatum, Poecilus versicolor, P. cupreus, Nebria brevicollis, Carabus granulatus*) made up 47.9 % (n = 44,231) of the total density and there were 35 species caught with only 1 specimen. See Appendix A2 for a complete species list including information on the traits for each species.

A main assumption of this study was that floodplain ground beetle FR should be higher than what could be expected by chance. Figure 2A displays the probabilities that an observed FR was higher than what would be found for the same community by simulation. One of the main results of this study were the low probabilities that ground beetle FR is higher than random. The probabilities were lowest immediately following the extreme flood in autumn 2002, and increased in spring seasons and with on-going time after the extreme flood. The highest probabilities were determined 40 months after the extreme flood in autumn 2005. Here, the average probability that a community possessed higher FR than random was around 62 %. Usually, the values varied between 30 % in autumn and 50 % in spring.

In other words, there were high probabilities that observed ground beetle FR was either smaller than, or completely random. To determine which exactly was the case, Figure 2B displays the amount of FR observed in the 48 communities that was significantly smaller than random, higher than random, or of random nature. There were almost no communities present immediately after the extreme flood, which showed FR values significantly higher than random. Even 1 year later, in autumn 2003, less than 5 % of the communities present possessed a significantly higher FR. In the following years, the number of significantly higher FR observations increased to about 10% in autumn and 20 % in spring, respectively. Nevertheless, on average, about 60 % of the communities showed a random FR, and there was no clear trend for this value to decrease with increasing time. In particular, in the first 2 autumn seasons following the flood there were relatively high numbers of communities with FR values significantly lower than could be expected by chance.

Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood



**Figure 2** Results of the null models to identify whether the observed FR differs from random expectations. (A) Probability that the observed FR is higher than random. Boxplots refer to the median, 25 % and 75 % quantiles of the probability values of the 48 sampling plots; (B) Number of communities with significant FR observations. Colours indicate that the observed FR was significantly higher (dark grey), significantly smaller (medium grey), or not significantly different (light grey) from random, respectively.

There were highly significant effects of total species number and the number of redundant species, respectively, on the amount of redundant species in floodplain ground beetle communities (Figure 3, Table 2). That is, species rich ground beetle communities have generally more redundant species, but also a higher amount of redundant species compared with species-poor communities. Results also show that communities must consist of more than 8 redundant species to achieve

### CHAPTER FIVE 98 Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood

FR levels of at least 50 %. The importance of time after the extreme flood for the FR of ground beetles was limited. FR significantly increased already after 2 sampling periods (month 9) and remained on that high level during the subsequent sampling periods. On average, each community studied here possessed around 40 % redundant species, except for in 2002, when only 20% redundant species could be detected. There was also a highly significant effect of habitat type on the FR of ground beetles, which was highest in habitats that are frequently flooded compared with elevated habitats with only minor flood disturbance history (Figure 3, Table 2).



**Figure 3** Relationships between explanatory variables and FR (number of redundant species in a community) of ground beetles based on non-linear (months after flood) and linear mixed effects models. Points refer to communities of each sampling period. Solid line represents the regression line based on the predicted values of the respective model. Habitat types: Gl.fresh = fresh grassland, Gl.moist = moist grassland, Gl.wet = wet grassland, \*\*p < 0.01, \*\*\*p < 0.001.

**Resilience through redundancy? Effects of functionally equivalent species on ground beetle functional diversity after an extreme flood** 

**Table 2** Variables and community properties explaining ground beetle FR. Results are based on linear or nonlinear mixed effects models with sampling plots as random effects. E = parameter estimate, SE = standard error, df = degrees of freedom, p = p-value, LME = linear mixed effects model, NLME = non-linear mixed effects model based on a Michaelis–Menten kinetics (Monod function). Gl.wet = wet grassland, Gl.moist = moist grassland. \*\*p < 0.01, \*\*\*p < 0.001.

Explanatory variables (type, scale)	Parameters	E	SE	df	р	Model type
Total number of species (continuous, counts)	Intercept	0.240	0.026	279	***	LME
	Slope	0.010	0.001	279	***	
Number of redundant species (continuous, counts)	Saturation (V <sub>m</sub> )	1.130	0.075	324	***	NLME
	MM-constant (K <sub>m</sub> )	10.251	1.174	324	***	
Time (categorical, months)	Saturation (V <sub>m</sub> )	0.468	0.045	324	***	NLME
	MM-constant (K <sub>m</sub> )	1.366	0.453	324	**	
Habitat type (3-fold categorical)	Intercept	0.333	0.038	280	***	LME
	Slope Gl.wet	0.180	0.029	45	***	
	Slope Gl.moist	0.086	0.030	45	**	

### Discussion

This study showed that ground beetle communities that experienced an extreme flood event and that quickly recovered in terms of their taxonomic structure (see Gerisch *et al.* 2012) also quickly recovered in terms of their functional redundancy. I consider this to be evidence of high functional resilience of ground beetles following an extreme flood. However, the results also support the expectations of many authors that functional redundancy (FR) cannot be the only stabilizing mechanism for communities experiencing extreme disturbances, but the number of species available is also important, as well as how they assemble, and how quickly they do so.

There are different perceptions on the extent of FR in various ecological systems and for different taxa, but in many studies it was observed to be lower than expected. For example, Petchey *et al.* (2007) found no redundancy in British bird communities and there are several studies that detected low or no redundancy in coral reef assemblages (Micheli & Halpern 2005; Sasaki *et al.* 2009; Laliberté *et al.* 2010; Guillemot *et al.* 2011) found differential patterns for plants, as they reported on increasing FR with decreasing grazing and land use intensity, respectively. Here, I also established that there were a considerable number of communities with significantly lower FR than expected, and some that did not significantly differ from random. These findings contradict our initial hypothesis, but also generally support much of the previous work.

The low FR observed immediately after the extreme flood can be explained by a combination of random post-flood colonization and existing trait dissimilarities among the surviving species. From previous studies I know that ground beetles can either hibernate during critical seasons or quickly evade disturbed plots as a result of their high mobility (Rothenbücher & Schaefer 2006; Bates et al. 2006; Lambeets et al. 2008). In our data there is evidence that the flood-surviving species used both strategies, and that they differed in their ecological requirements, their morphology, and in their lifehistory characteristics. The combination of random re-colonization by few species that are functionally different implies little likelihood that functionally similar species would meet on a certain plot, and this therefore caused relatively low FR immediately after the flood. With ongoing time, however, stochastic arrival processes were reduced and local regulating forces, such as periodic flood disturbance, controlled community assembly thereafter. Similar findings were also reported by Jenkins & Buikema (1998) for the succession of zooplankton in ponds. In our case, the shift from random to directed colonization has led to an increase of functionally similar species, particularly in the spring season when floods normally occur, because the changing habitat template has shaped the trait requirements, and hence sorted the species with similar functional attributes (Lambeets et al. 2008; Gerisch 2011). In other words, the increase in significantly higher FR observations in spring and with time reflects both, the effects of the habitat templet and a reduction in post-flood entropy in functional and taxonomical community composition.

However, there might also be different explanations for the high number of random observations. Null models should be based on artificial communities containing species from a regional species pool (Chase *et al.* 2011). Here, our regional species pool comprized mainly typical floodplain grassland species, but it lacks several species that are not primarily bound to periodically flooded wetlands (e.g. strict forest or dryland species). The consequence is that the average FR observed is, in many cases, similar to what one would expect, because the artificial communities are quite similar to the observed ones. Despite this, FR was found to be significantly higher than random in specific habitats (e.g. frequently flooded oxbows) and particularly in the spring season, suggesting that it is of some importance under specific conditions. Some refer to this as ecological insurance against the breakdown of community functioning (Yachi & Loreau 1999), because the disturbance-induced loss of species can be compensated for by the presence of functionally redundant species.

Theory also predicts that resilience should increase with increasing functional redundancy among the species (Walker, Kinzig & Langridge 1999; Rosenfeld 2002). However, most of this work is theoretical and there are only a few empirical studies available tackling this research field (e.g. Bellwood, Hoey & Choat 2003; Micheli & Halpern 2005; Petchey et al. 2007). A reason for this lack of interest might also be the existing critics of the entire concept of FR. Some authors argue that FR seems incompatible with classical niche theory and the stable coexistence of species (Loreau 2004; Resetarits & Chalcraft 2007), while others predict that not trait differences, but random dispersal, survival, and reproduction, control community patterns (Hubbell 2006). This rather critical view is aggravated by the fact that FR is often not detectable or is lower than expected. My study stands between the supportive and the contradictory opinions, demonstrating that FR can be seen as an important part of community resilience, but that it is likely not to be a simple linear relationship. The overall community resilience, not only functional resilience as studied here, depends on different controlling agents under different environmental conditions or successional stages of the habitat. For example, found that bee communities frequently exposed to fire events showed higher functional diversity, and also a higher FR. They linked this relationship to high resilience, as it allows for a stable functional rebuilding of the communities after fire events. Other work showed contrary results. For example, Sasaki et al. (2009) reported on lower FR of plants in harsh environmental conditions and supposed that species under such conditions are generally better suited to environmental stress and, therefore, trait complementarity rather than redundancy stabilizes communities. In addition, Laliberté et al. (2010) found decreasing FR with increasing environmental stress, and increased vulnerability of the remaining species for future disturbances, i.e. decreasing community resistance and resilience. These contrary empirical findings indicate that the diversity-stability debate of the last decade is still not fully solved and that habitator taxa-specific relationships exist.

On the other hand, almost all studies in this field note that abrupt losses of certain (keystone) species and the decrease of functional diversity below a certain threshold can have a serious impact on the functioning of entire communities. Here we confirm these findings, as I showed that rapid taxonomic changes following extreme floods (see previous study of Gerisch et al. 2012) also involved a massive decline in FR, which is a sign of low functional resilience on a very short-term scale. Hence I assume that FR is not a primary mechanism to buffer the effects of extreme events, because all species are similarly affected and usually cannot cope with such weather extremes. Especially following extreme disturbances, immigration and recolonization processes might be of higher importance for community recovery than the functional equivalence of the few surviving species. This means that the capacity of ground beetles to re-establish a network of processes and properties that ensure the overall performance and a basic ecological structure of the community depends not only on FR per se, but also on the intensity of the disturbance, priority effects, and certainly on time. Nevertheless, I still know little about the roles that particular species or variables have for community functioning, and much work, in addition to this study, relates only limited sets of biological traits to processes or properties that I consider to be important for ecological functioning. Therefore, further effort needs to be put into basic questions of ecology, for example to reveal relevant traits for specific properties such as resilience, better transfer theoretical background into empirical studies, and find appropriate ways to generalize among the diversity of taxa, ecosystems, and stress agents.

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Species	ło	Indi <sup>v</sup> sam]	vidua. pling	l num seaso	lbers i n	g			Life-hi	story tr	aits			Ecolo prefe	gical	30
	Total Number Individuals	2002 nmutuA I	II Spring 2003	E002 nmutuA III	VI Spring 2004	4002 nmutuA V	VI Spring 2005	2005 nmutuA IIV	Worphology Worphology	Mode of Overwintering	(mm) əzis yboð	Vivitos ylieD	əbom pnibəə7	Humidity Preference	Light Preference	Habitat Preference
Acupalpus dubius	2	0	0	0	0	0	2	0	mac	ad	2.7	diu	car	Ч	unsh	eur
Acupalpus exiguus	378	0	е	1	197	6	161	7	mac	ad	2.7	diu.noc	car	Ч	unsh	ste
Acupalpus parvulus	10	0	0	0	č	0	7	0	mac	ad	3.7	diu	car	Ч	unsh	eur
Agonum emarginatum	14050	T	1675	40	4696	52	7567	19	mac	ad	7.2	noc	car	ч	m.sh	eur
Agonum dolens	15	5	e	0	e	0	4	0	mac	ad	8.8	noc	car	Ч	unsh	ste
Agonum duftschmidi	1858	0	368	2	405	4	1077	2	dm	ad	8.3	noc	car	Ч	p.sh	ste
Agonum fuliginosum	30	0	7	0	7	8	8	0	dm	ad	6.7	noc	car	Ч	p.sh	eur
Agonum lugens	48	0	+	1	34	1	6	2	mac	ad	9.1	noc	car	Ч	p.sh	ste
Agonum marginatum	132	0	97	7	7	0	27	0	mac	ad	9.2	diu	car	ч	unsh	eur
Agonum micans	2423	9	675	е	309	8	1421	1	mac	ad	6.7	noc	car	Ч	unsh	eur
Agonum muelleri	1	0	0	0	0	0	1	0	mac	ad	8.2	diu	car	Е	unsh	eur
Agonum piceum	48	0	7	0	17	1	29	0	mac	ad	6.4	noc	car	h	p.sh	eur
Agonum sexpunctatum	5	0	2	0		0	2	0	mac	ad	8.2	diu	car	Ч	unsh	eur
Agonum thoreyi	2	0	0	0	0	1	т Т	0	mac	ad	6.9	diu.noc	car	Ч	p.sh	ste
Agonum versutum	781	6	103	Э	192	1	472	1	mac	ad	7.6	diu	car	h	unsh	eur
Amara aenea	27	0	с	0	12	0	12	0	mac	ad	7.5	diu.noc	phy	×	unsh	eur
Amara apricaria	4	0	0	0	0	4	0	0	mac	lar	7.5	noc	poly	E	unsh	eur
Amara aulica	61	0	0		2	7	9	45	mac	lar	12.7	noc	phy	ε	unsh	eur
Amara bifrons	14	0	0	5	0	5	0	4	mac	lar	6.4	noc	phy	×	unsh	eur

**Appendix A2** 1/8 Full list of species used in chapter five, including life-history traits and ecological preferences. mac = macropterous, br = brachypterous, dm = dimorph, ad = adult, lar = larvae, diu = diurnal, noc = nocturnal, car = carnivo-rous, phy = phytophagous, poly= polyphagous, h = hygrophilous, m = mesophilous, x = xerophilous, m.sh = mainly.shaded, p.sh = partly.shaded, unsh = unshaded, eur = eurytopic, ste = stenotopic. For references on trait data see Appendix A2.

### Appendices

Appe	endix A2 2/8																				
	Habitat Preference	eur	eur	ste	eur	eur	eur	eur	ste	eur	eur	eur	ste	eur	eur	eur	eur	ste	eur	eur	ste
gical rences	Light Preference	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	p.sh	p.sh	p.sh	unsh
Ecolog	Humidity Preference	ш	×	×	×	ш	E	E	×	×	Ч	ш	Ч	×	ш	Ч	Ч	Ч	E	ш	ч
	əbom pnibəə7	phy	phy	phy	phy	phy	poly	phy	phy	phy	phy	phy	phy	phy	poly	poly	poly	car	car	car	car
	ytivitse ylieD	diu	diu	noc	diu	diu	diu	noc	noc	diu	diu	diu	diu	diu	noc	noc	noc	diu.noc	diu	noc	noc
its	(mm) əzis yboð	6.9	7.8	10.9	10.8	6.6	7.7	8.7	6.6	8.6	7	8.8	6	5	6.7	11.1	12.1	4.5	5.2	5.5	4.8
tory trai	Mode of Overwintering	ad/lar	ad	lar	ad/lar	ad	lar	lar	lar	ad	ad	ad	ad	ad	ad	ad	lar	ad	ad/lar	ad	ad
Life-his	Morphology Wing	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac	mac
	NII Autumn 2005	50	0	55	0	5	51	0	0	0	4	3	5	2	0	241	0	1	0	0	0
	VI Spring 2005	197	0	5	0	15	60	0	0	11	11	18	83	2	0	346	0	265	0	1	0
	4002 nmutuA V	71	0	79	4	0	124	0	0	12	22	31	7	0	0	129	2	1	0	с	0
oers in	1V Spring 2004	365	m	2	0	5	573	0	0	14	32	18	204	1	1	181	0	133	1	4	
num} seasor	5002 nmutuA III	8	m	109	0	0	37	1	0	2	7	2	7	0	0	25	0	1	0	2	
vidual pling s	II Spring 2003	56		0	0	4	381	0	0	2	29	6	93	0	0	85	0	78	1	1	2
Indi sam]	S00S nmutuA I	1	0	e	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
ło	Total Number Individuals	748	7	253	4	29	1226	1	1	41	105	81	399	5	1	1007	2	479	2	11	4
Species		Amara communis	Amara convexior	Amara equestris	Amara eurynota	Amara familiaris	Amara lunicollis	Amara majuscula	Amara municipalis	Amara ovata	Amara plebeja	Amara similata	Amara strenua	Amara tibialis	Anchomenus dorsalis	Anisodactylus binotatus	Anisodactylus signatus	Anthracus consputus	Asaphidion pallipes	Badister bullatus	Badister collaris

# CHAPTER FIVE 105 Appendices

Appen	$\mathbf{d1X} \mathbf{A2} \ \mathbf{5/8}$																				
	Habitat Preference	ste	ste	eur	ste	eur	ste	ste	eur	ste	eur	eur	ste	ste	ste	ste	eur	eur	eur	eur	ste
gical rences	Light Preference	p.sh	p.sh	m.sh	p.sh	p.sh	m.sh	m.sh	unsh	unsh	p.sh	unsh	unsh	m.sh	p.sh	p.sh	m.sh	unsh	p.sh	unsh	unsh
Ecolo prefe	Humidity Preference	h	Ч	Ч	Ч	Ч	h	Ч	Ч	h	Ч	Ч	h	h	Ч	Ч	h	ш	Ч	Ч	Ч
	əbom pnibəə7	car	car	car	car	car	car	car	car	car	car	car	car	car	car	car	car	car	car	car	car
	ytivitse ylieD	diu	noc	noc	noc	noc	noc	diu	diu	diu	diu	diu	noc	noc	diu	diu	diu	diu	diu	diu	diu
its	(mm) əzis yboð	5.6	5.6	6.5	6.8	4.3	8	6.5	3.3	3.2	4.1	4.7	5.6	3.5	3.9	2.8	3.3	3.6	3.7	2.8	3.7
tory trai	Mode of Overwintering	ad	ad	ad	ad	ad	ad	ad	ad	ad	ad	ad	ad/lar	ad	ad	ad	ad	ad	ad	ad	ad
Life-his	Wing Worphology	mac	mac	mac	mac	dm	mac	mac	mac	dm	mac	mac	mac	mac	mac	dm	dm	dm	mac	mac	mac
	nmutuA IIV 2005	0	0	0	1	0	3	0	0	6	40	0	81	0	2	8	12	2	1	0	0
	VI Spring 2005	0	0	0	4	7	9	1	0	14	600	1	643	0	1	38	381	4	5	1	0
	4002 nmutuA V	0	0	0	0	0	10	0	0	0	48	0	149	0	0	4	20	0	0	0	0
bers in	IV Spring 2004	1	0	2		5	6	1	0	ю	673	0	220	0	0	47	317	1	7	0	0
l numl seasor	E002 nmutuA III	0	0	0	0	0	2	0	0	0	16	0	154	0	0	0	0	0	2	0	0
ividua	II Spring 2003	6		0	2	1	12	0	1	1	244	0	672	1	0	5	25	0	5	0	2
Indisam	2005 nmutuA I	0	0	0	0	0	1	0	0	0	0	0	6	0	0	0	0	1	0	0	0
ło	Total Number Individuals	10	1	2	8	13	43	2	1	27	1621	1	1928	1	e	102	755	8	20	1	2
Species		Badister dilatatus	Badister dorsiger	Badister lacertosus	Badister meridionalis	Badister sodalis	Badister unipustulatus	Bembidion argenteolum	Bembidion articulatum	Bembidion assimile	Bembidion biguttatum	Bembidion bruxellense	Bembidion dentellum	Bembidion doris	Bembidion fumigatum	Bembidion gilvipes	Bembidion guttula	Bembidion lampros	Bembidion lunulatum	Bembidion minimum	Bembidion obliquum

## CHAPTER FIVE 106 Appendices

Appendix A2 4/8																			
	Habitat Preference	eur	eur	eur	eur	ste	eur	eur	eur	ste	eur	eur	eur	eur	ste	eur	eur	ste	ste
gical rences	Light Preference	p.sh	unsh	unsh	unsh	unsh	unsh	p.sh	unsh	unsh	p.sh	hsnu	unsh	hsnu	m.sh	m.sh	unsh	hsnu	unsh
story traits Ecolo prefe	Humidity Preference	meso	4	Ч	ε	ч	Ч	Ч	h	Ч	×	×	×	×	Ч	Ч	Ч	Ч	ч
	əbom pnibəə7	poly	car	car	car	car	car	car	car	car	poly	poly	poly	poly	car	car	car	car	car
	ytivitse ylieD	diu.noc	diu	diu	diu	diu	diu	diu	diu	diu	noc	noc	noc	diu	diu.noc	noc	noc	diu	diu
	(mm) əzis yboð	3.1	2.6	4	3.1	3.7	3.8	5.3	4.4	11.8	4.4	11.8	7.6	23.6	28.1	19.5	23.1	11.1	11.8
	Mode of Overwintering	ad	ad	ad	ad	ad	ad	ad	ad	ad	lar	lar	lar	ad	ad/lar	ad	ad	ad	ad
ridual numbers in Life-his bling season	Werphology Worphology	dm	mac	dm	mac	mac	mac	dm	dm	mac	dm	br	dm	br	br	dm	br	mac	mac
	111 Autumn 2005	0	0	0	1	0	0	4	0	0	1	113	52	0	11	427	4	1	0
	VI Spring 2005	0	2	8	с	0	19	10	1	14	0	1	0	2	1	2141	14	623	1
	4002 nmutuA V	0	0	1	e	0	0	11	0	0	1	112	44	0	0	187	7	0	0
	IV Spring 2004	1	2	12	6	0	с	12	0	2	0	1	1	7	0	1093	10	210	12
	5002 nmutuA III	0	0	0	1	1	0	2	0	0	0	9	20	0	0	16	0	1	0
	II Spring 2003	0	0	7	4	0	5	9	13	0	0	0	0	З	0	829	0	275	1
Indiv samp	2002 nmutuA I	1	0	1	5	0	1	1	0	1	0	0	1	0	0	1	1	0	0
Total Number of Individuals		2	4	29	26	1	28	46	14	17	2	233	118	12	12	4694	36	1110	14
Species		Bembidion obtusum	Bembidion octomaculatum	Bembidion properans	Bembidion quadrimaculatum	Bembidion quadripustulatum	Bembidion semipunctatum	Bembidion tetracolum	Bembidion varium	Blethisa multipunctata	Bradycellus harpalinus	Calathus fuscipes	Calathus melanocephalus	Carabus auratus	Carabus glabratus	Carabus granulatus	Carabus nemoralis	Chlaenius nigricornis	Chlaenius tristis

# CHAPTER FIVE 107 Appendices
Appe	endix A2 5/8																				
	Habitat Preference	eur	eur	ste	eur	ste	eur	eur	eur	eur	eur	eur	eur	eur	ste	eur	eur	ste	eur	eur	eur
gical	Light Preference	p.sh	m.sh	unsh	p.sh	unsh	p.sh	unsh	p.sh	unsh	unsh	p.sh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh	unsh
Ecolog prefer	Humidity Preference	ч	Ч	Ч	h	h	Ч	Ч	Ч	×	h	h	×	×	×	h	×	×	×	×	×
	əbom pribəə7	phy	car	car	phy	car	car	car	car	car	car	car	poly	poly	poly	poly	poly	poly	poly	poly	poly
	Vaily activity	noc	noc	diu	diu	diu	diu	diu	diu	diu	diu	noc	noc	diu	noc	diu	diu	noc	noc	noc	diu
its	(mm) əzis yboð	6.1	16	4.6	8.8	3.2	2.6	3.7	2	8.3	6.8	3.7	10.3	9.6	9.2	9.6	7.1	6.2	5.4	10.1	9.6
story tra	Mode of Overwintering	ad	ad/lar	ad	ad	ad	ad	ad	ad	ad	ad	lar	ad	ad/lar	ad	ad/lar	ad	ad	ad	ad/lar	ad
Life-his	Worphology Worphology	dm	br	dm	mac	mac	dm	mac	mac	mac	mac	br	mac	mac	mac	mac	mac	dm	br	mac	mac
	VII Autumn 2005	70	1	0	0	0	12	0	0	0	0	46	1	2	0	4	1	0	0	0	0
	VI Spring 2005	1122	0	5	0	7	21	19	35	0	13	9	10	0	0	62	24	0	0	0	0
	4002 nmutuA V	53	0	9	0	0	10	1	0	0	0	5	з	0	1	4	4	0	0	1	0
oers in	1V Spring 2004	816	0	2	0	3	32	с	15	0	1	1	12	13	0	32	17	1	1	1	<del>, ,</del>
l numb seasor	5005 nmutuA III	23	0	0	1	0	0	0	0	0	0	0	0	0	1	1	с	0	0	0	0
ividua pling	II Spring 2003	69	0	1	4	0	0	0	6	0	17	0	с	0	0	20	8	0	0	1	0
Indis	2002 nmutuA I	16	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0
Total Number of Individuals		2169		14	5	10	76	23	59	1	92	58	29	15	2	124	57	1	1	с	Ţ.
Species		Clivina fossor	Cychrus caraboides	Demetrias monostigma	Diachromus germanus	Dyschirius aeneus	Dyschirius globosus	Dyschirius luedersi	Elaphropus parvulus	Elaphrus cupreus	Elaphrus riparius	Epaphius secalis	Harpalus affinis	Harpalus distinguendus	Harpalus froelichii	Harpalus latus	Harpalus luteicornis	Harpalus picipennis	Harpalus pumilus	Harpalus rubripes	Harpalus rufipalpis

#### CHAPTER FIVE 108 Appendices

Appendix A2 6/8																					
	Habitat Preference	eur	eur	eur	eur	ste	eur	eur	eur	ste	ste	ste	eur	eur	eur	eur	ste	eur	ste	eur	ste
gical ences	Light Preference	unsh	m.sh	unsh	m.sh	unsh	unsh	p.sh	m.sh	unsh	unsh	unsh	unsh	unsh	p.sh	m.sh	unsh	m.sh	p.sh	p.sh	p.sh
Ecolog prefei	Humidity Preference	×	Ч	×	Ч	×	×	Е	h	h	h	h	×	×	×	h	h	h	Ч	h	٩
	əbom pnibəə7	poly	car	car	car	car	car	car	car	car	car	car	phy	phy	phy	car	car	car	car	car	car
	Vaily activity	noc	noc	diu	noc	diu	diu	diu	diu	diu	noc	diu.noc	diu	diu	noc	noc	diu	noc	noc	noc	noc
ts	(mm) əzis yboð	6.8	7.4	3.3	12.1	4.8	5.1	4.8	5	6.8	5.5	8.5	11.3	8.3	7.8	5.6	8.1	8.6	3.3	10.5	6
tory trai	Mode of Overwintering	ad	ad	ad	lar	ad/lar	ad/lar	ad	ad	ad	ad/lar	ad	ad	ad/lar	ad/lar	ad/lar	ad	lar	ad	ad	ad
Life-his	Morphology Wing	mac	mac	br	mac	dm	dm	dm	dm	mac	mac	mac	mac	mac	mac	dm	mac	br	dm	mac	mac
	nmutuA IIV 2005	0	12	1	1035	0	1	0	0	0	0	106	4	0	23	64	0	86	1	3	0
	VI Spring 2005	2	659	9	837	0	0	0	œ	1	1	260	0	0	45	6	0	15	4	157	16
	+002 nmutuA V	0	0	12	2065	0	0	0	0	0	0	64	0	1	13	44	7	62	0	2	0
oers in	IV Spring 2004	9	159	106	1775	0	0	1	e	1	0	228	0	0	e	23	14	22	2	22	m
numk season	5002 nmutuA III	0	16	7	580	0	0	0	1	0	0	29	0	0	0	31	1	72	0	6	0
vidual pling s	II Spring 2003	0	1919	1	276	0	0	1	4	0	0	240	0	0	1	13	8	З	0	79	1
Indisam	2002 nmutuA I	0	37	0	56	1	0	0	0	0	0	0	0	0		0	0	9	0	0	0
ło	Total <sup>N</sup> umber Individuals	8	2802	133	6624	1	1	2	11	2	1	927	4	1	86	184	30	266	7	272	20
Species		Harpalus signaticomis	Loricera pilicomis	Microlestes minutulus	Nebria brevicollis	Notiophilus aesthuans	Notiophilus aquaticus	Notiophilus biguttatus	Notiophilus palustris	Odacantha melanura	Omophron limbatum	Oodes helopioides	Ophonus diffinis	Ophonus puncticeps	Ophonus rufibarbis	Oxypselaphus obscurus	Panagaeus cruxmajor	Patrobus atrorufus	Philorhizus sigma	Platynus assimilis	Platynus livens

### CHAPTER FIVE 109 Appendices

Appendix A2 7/8																			
	Habitat Preference	ste	eur	eur	ste	ste	eur	eur	ste	eur	eur	eur	eur	eur	eur	eur	eur	eur	eur
gical ences	Light Preference	m.sh	unsh	unsh	unsh	unsh	unsh	m.sh	p.sh	unsh	p.sh	p.sh	m.sh	m.sh	p.sh	p.sh	m.sh	p.sh	unsh
Ecolog	Humidity Preference	Ч	h	æ	×	×	X	Ч	h	h	ш	ш	h	h	Ч	h	h	Ч	Ч
	əbom pnibəə7	car	poly	car	poly	poly	poly	poly	car	poly	poly	poly	poly	car	car	car	poly	poly	poly
	Vəivitya ylisd	noc	diu	diu	noc	noc	noc	noc	diu.noc	noc	noc	noc	diu.noc	noc	noc	noc	noc	noc	noc
ts	(mm) əzis yboð	13	11.6	10.2	12.2	10.1	13.4	11.3	5.7	9.1	13	15.4	7.4	18.4	10.8	9.7	6.1	6.9	5.7
tory trai	Mode of Overwintering	ad	ad	ad	lar	lar	ad/lar	ad	ad	ad	ad	lar	ad	lar	ad	ad	ad	ad	ad
Life-his	Morphology Wing	mac	mac	mac	mac	mac	mac	dm	dm	mac	mac	dm	dm	dm	dm	br	dm	dm	mac
	nmutuA IIV 2005	0	160	768	0	0	26	139	0	70	0	1388	1	30	10	1	73	94	27
	VI Spring 2005		681	2870	0	2	307	761	5	501	0	336	11	1	521	1	273	36	688
	4002 nmutuA V	0	285	1148	0	0	61	85	0	18	0	473	0	51	14	0	129	127	11
ers in	1V Spring 2004	0	1376	2068	H	0	28	683	1	278	0	165	7	9	112	0	237	83	39
numb season	5002 nmutuA III	0	308	89	Ţ	0	166	85	0	14	1	781	1	36	12	0	4	15	9
vidual pling s	II Spring 2003		841	395	0	0	30	217	0	136	0	115	2	7	123	0	20	47	46
Indi <sup>s</sup> samj	S00S nmutuA I	0	1	0	0	0	ε	0	0	0	0	56	0	28	0	0	1	0	0
îo	Total <sup>N</sup> umber Individuals	2	3652	7338	2	2	621	1980	9	1070	1	3314	22	159	792	2	737	402	817
Species		Platynus longiventris	Poecilus cupreus	Poecilus versicolor	Pseudoophonus calceatus	Pseudoophonus griseus	Pseudoophonus rufipes	Pterostichus anthracinus	Pterostichus diligens	Pterostichus gracilis	Pterostichus macer	Pterostichus melanarius	Pterostichus minor	Pterostichus niger	Pterostichus nigrita	Pterostichus rhaeticus	Pterostichus strenuus	Pterostichus vernalis	Stenolophus mixtus

#### CHAPTER FIVE 110 Appendices

Арре	endix A2 8/8											
	Habitat Preference	ste	eur	eur	eur	eur	ste	eur	eur	eur	eur	ste
gical rences	Light Preference	unsh	unsh	p.sh	unsh	unsh	m.sh	m.sh	m.sh	p.sh	unsh	p.sh
Ecolo	Humidity Preference	٩	Ч	Ч	×	ш	Ч	ч	Ч	ш	Ч	×
	əbom pnibəə7	poly	poly	car	n.a.	poly	car	car	car	car	car	phy
	Vaivitos ylieO	noc	noc	noc	diu	noc	noc	noc	noc	noc	noc	noc
uits	(mm) əzis yboð	6.2	6.3	7.5	2.9	7.4	2.2	4.3	3.9	3.6	4.8	14.2
story tra	Mode of Overwintering	ad	ad	lar	ad	lar	ad	ad	lar	ad/lar	ad	lar
Life-hi	Werphology Morphology	mac	mac	br	dm	dm	mac	mac	dm	mac	mac	mac
	nmutuA IIV 2005	25	0	0	0	0	0	1	17	464	0	0
	VI Spring 2005	62	0	10	9	0	17		0	ю	2	0
	4002 nmutuA V	0	0	0	0	0	0	1	28	446	0	
ers in	1V Spring 2004	39	3	0	46	0	10	0	0	9	2	0
numb eason	E00S nmutuA III	0	0	0	0	1	0	0	0	75	0	14
vidual siing s	II Spring 2003	6	1	2	0	0	1	0	0	8	0	0
Indiv samj	2002 nmutuA I	0	0	0	0	1	0	0	1	1191	0	0
îo	rotal Number Individuals	135	4	12	52	2	28	3	46	2193	4	15
Species		Stenolophus skrimshiranus	Stenolophus teutonus	Stomis pumicatus	Syntomus truncatellus	Synuchus vivalis	Tachys bistriatus	Trechoblemus micros	Trechus obtusus	Trechus quadristriatus	Trichocellus placidus	Zabrus tenebrioides

#### CHAPTER SIX Synopsis

The dissertation described in the previous five chapters provides a broad picture of the ecological response of ground beetles to an extreme flood event. This final chapter aims to summarize and synthesize the key findings of the thesis, with a major emphasis on explaining the role of taxonomical and functional shifts of ground beetles for ensuring community functioning, even under extreme environmental conditions.

Key finding 1: Post-flood resilience depends on mobility, habitat generality & priority effects

Two expectations have been raised in the course of this study: (1) The extreme flood caused a massive species breakdown of ground beetles and (2) ground beetles quickly recovered from this event in terms of species richness, composition, and diversity. As expected, we found tremendous species turnovers, declines of species and individuals, and significantly lower species diversity levels following the extreme flood event in 2002. We also found that ground beetle communities quickly recovered to pre-flood structures, which can be explained by their high dispersal capacity and their habitat generality. The resilience of particular species was, however, impeded due to pronounced priority effects.

Based on the results of chapters two and three, I conclude that taxonomical resilience of ground beetles after extreme floods is not a linear process, but is contingent on several factors acting on different response levels. Unlike other taxonomical groups, ground beetles experienced a massive breakdown of species and individuals (see Ilg et al. 2008a & Ilg et al. 2008b for other groups). Therefore, the results provide evidence that ensuring immediate resistance, for example based on special resistance traits, is not a suitable strategy for the species to survive such extreme events. The work from chapter two suggests that it is more effective for floodplain ground beetles to invest in mobility and recolonization power than in particular resistance strategies. In an evolutionary context, floodplain biodiversity has always faced extreme events and adapting to those rare occurrences would limit the fitness of many species during normal, regular flooding. Interestingly, this is not true for all taxonomical groups, as effective resistance strategies can be found in other organisms which are less mobile than ground beetles. For example, special roots enable plants to withstand physical stress and to survive for long periods under water. Also terrestrial molluscs can outlast floods for a considerable time and it is known that individuals are relocated rather than killed by flood events, which may be seen as high community resistance (Ilg et al. 2011). For ground beetles, this implies that adapting to regular flooding is a compromise species must make in fluctuating environments, taking the risk that highly stochastic events cannot be coped with.

Recolonization goes along with high mobility of the species, and only a few months after the extreme flood many species had immigrated back into the floodplain. Habitat generalist species, in particular, invaded quickly, and some of these even established with higher abundances than before the flood. In contrast, it took considerably longer for some true floodplain species to recover to pre-flood conditions. This is a sign that priority effects, i.e. the impacts of early-arriving species on those arriving later in a system, shaped the way ground beetle communities recovered from flooding. The early-arriving generalists are competitive in different floodplain habitats because they can also cope with some amount of hydrological variation. Moreover, as they are not strictly bound to floodplain habitats, their larvae were not affected by the extre-

me flood. Generalists therefore outperformed many floodplain specialists in the early stages after the flood and decelerated their recovery, simply by their quick population growth. With time, existing priority effects were diminished and replaced by permanent effects of the habitat templet. That is, the competitive advantage of many generalist species appearing immediately after disturbances decreased with the ongoing leveling of the extreme event effects. In chapter three, I found that under normal flooding conditions especially species with small body size and reproduction in spring are most abundant in habitats with high hydrological variation. This proves current knowledge that ground beetles, like many other floodplain invertebrates, follow a risk strategy which involves producing many offspring and being highly mobile in periods of high environmental variability (Weigmann & Wohlgemuth-von Reiche 1999).

Ultimately, almost no difference between pre- and post-flood communities could be detected after four years of flooding, although recovery within these periods was driven by several species turnovers and non-linear succession pathways. That is, resilience varied among different temporal scales. This might be an important implication for future trends, because recovery processes could lie between decreasing intervals of aperiodic extreme events. Hence, increased frequencies of extreme events have the potential to disrupt recovery processes and to either keep communities in a transition state or to force species adaptation to extreme events. For now, it is not really clear how these predictions fit into an evolutionary framework and how species communities will taxonomically and functionally change under such conditions.

**Key finding 2:** Trait homogenization as an effective strategy for ground beetles to cope with regular flooding

As already addressed, morphological and life-history adaptations play important roles for ground beetles in dynamic landscapes. Recent work, including this thesis, found that body size, overwintering strategy, and wing morphology is crucial to ground beetles' ability to cope with floodplain dynamics (Rothenbücher & Schaefer 2006; Lambeets *et al.* 2008). Predictions of traits-based theories (Southwood 1988; Poff 1997; Statzner *et al.* 2004) imply that species traits will be homogenized when environmental stress increases, resulting in similar survival strategies of species. We used functional diversity, an integrative multi-trait approach, to test this assumption and to estimate how increasing hydrological disturbance can change the richness, range, and distribution of traits in ground beetle communities. Our primary hypothesis was that increasing flood disturbance will cause species traits to converge and therefore lead to a decrease of many facets of functional diversity.

The work presented in chapter four reports a rarely observed inverse relationship between flood disturbance, species diversity, and different components of functional diversity: while species richness and evenness increased, functional dispersion, evenness, and divergence measures significantly decreased at high disturbance levels. *Functional dispersion* is the mean distance in trait space of individual species to the centroid of all species and can therefore describe the degree of trait homogenization. It proves our main assumption that only specific trait combinations remain suitable for ground beetles to cope with rapidly increasing disturbance intensities. In our study, *functional evenness* indicates the degree to which abundant and functionally different species invaded communities. The low functional evenness observed at highly flood-disturbed sites indicates that species with different functional characters can also exist on these frequently flooded habitats. But we also believe that those species, mainly habitat generalists,

can only survive in such habitats for short periods of low flooding intensity. The decreasing *functional divergence* observed indicates that although total species richness increased and generalists skewed the abundance distribution in trait space, most of the species use the same 'mainstream' life-history strategies to cope with flood disturbance. In general, the results from chapters two and three suggest that trait filtering mechanisms cause high functional similarity of species inhabiting frequently disturbed habitats and supported not only the main hypothesis but also existing ecological theories.

Chapters three and four describe the survival strategies of floodplain ground beetles under normal hydrological conditions. This is a cornerstone for predicting the effectiveness of these strategies also during extreme events, which will be the explicit focus in chapter five and in another publication currently in preparation (Agostinelli et al. in prep). In the work presented here we found that some of the traits that enable ground beetles to survive hydrological dynamics are more strongly related to the timing of floods (e.g. reproduction, overwintering mode) than others (e.g. wing morphology, body size). Because the 2002 extreme flood was an aperiodic event, timing in particular is assumed to be one of the main agents causing structural and functional changes in ground beetle communities. Based on the outcomes of chapter three I conclude that species which develop in summer are most vulnerable to extreme summer floods because their larvae are intolerant to hydrological stress, which causes high mortality and inhibits rapid population recovery (Hering et al. 2004). This also explains the pronounced recovery lags of some of those species observed in chapter two. Not surprisingly, most of these were true floodplain species, which also suggests that some of the evolutionarily developed survival strategies may not be effective for maintaining community structures in the course of extreme floods. It can also be concluded that the close gearing of species adaptations to regular flood timing represents a weak spot for many species during extreme events. However, as outlined above, I consider this as a trade-off between investing in a perfect survival strategy and maintaining community functioning, taking the risk that populations may break down temporarily.

Trait homogenization is evidently an adaptive consequence of increasing habitat disturbance. However, although it is an effective strategy to establish in habitats characterized by regular flooding, stochastic extreme events can obviously not be buffered by this mechanism. Schweiger *et al.* (2007) showed that some kinds of disturbances cause non-random extinctions because they have similar effects on different species. This is especially true if species are functionally similar and respond in similar ways to habitat changes. Based on chapter four we expect this also to be true for this study because functional similarity was relatively high among the species, suggesting the high vulnerability of the species against the flood. That being said, the results also allow one to assume that if extreme events are temporarily separated and if they match the recovery times of populations, their effects should be averaged over a medium or long-term scale, and are therefore negligible for communities from an evolutionary perspective.

**Key finding 3:** Functional redundancy cannot ensure community functioning during extreme flood events

A major task of this thesis was to identify resilience of ground beetles to an extreme flood event. In chapter two, we found a comparably high taxonomical resilience, with only some small differences in species composition a few years after the flood. Recently, the focus was widened to measure resilience in a functional framework, where it is not the taxonomical dissimilarities to reference conditions that are at the center of interest, but how changing taxonomical compositions affect the functional diversity of a community. In this context, a community is considered resilient if it features a high proportion of species whose loss would not cause a decrease in functional diversity. This is also known as functional redundancy (Walker 1992; Rosenfeld 2002) and it means that resilient communities would perform in a similar way, even if some species are lost from the system. In chapter four we showed that under normal flooding regimes high levels of flood disturbance are related to higher species numbers but also a higher functional similarity among the species, suggesting high functional redundancy and thus high functional resilience. In chapter five I tested whether functional resilience is also important for ground beetles to withstand an extreme flood event. Based on the results of chapter four I hypothesized that this cannot be the case because of the intensity and the timing of the flood.

Similarly to the high taxonomical resilience of ground beetles after the extreme flood, I also found the species to be highly resilient from a functional perspective. That is, immediately after the flood there was only a small number of functionally redundant species present in the communities, which, however, quickly increased with time. However, although the general patterns of functional and taxonomical resilience are similar, the results from chapters two and five cannot be compared directly. The first study describes taxonomical differences of communities to previous conditions, which is also known as beta-diversity. In the latter study I analyzed how the capacity of a community to maintain its functioning changed after an extreme flood. The purpose of chapter five was therefore not to compare pre- and post-flood functional diversity, but to test the assumption that functional redundancy can stabilize community functioning, even if the communities face an extreme flood event (Petchey & Gaston 2009; Dalerum et al. 2010). Because I found low FR levels immediately after the flood and significantly higher FR values during normal flooding periods, the main finding is that functional redundancy cannot insure community functioning when extreme floods occur. The most plausible reason for this is that the extreme flood caused non-random extinctions among all species present, which likewise proved our earlier findings that trait sorting mechanisms lead to a homogenization of ground beetle traits (chapter three) and this suggests that similar species also respond in a similar way to environmental disturbance (chapter four).

I infer that FR can be an ecological trap during extreme events, where environmental conditions either exceed the coping range of the species, or where the adaptations do not match environmental conditions because of their close connection to timing. The trap effect is, nevertheless, limited under a scenario where extreme events occur only once or twice in a century because regeneration time would lie in between and being functionally synchronized with spring floods is a net positive balance, even if extreme floods occur sporadically. This means that although FR cannot effectively buffer extreme flood effects, it is still – among others – an important species property to ensure ground beetle functioning during regular flooding.

#### **Concluding remarks**

Reflecting the ecological complexity of floodplain biodiversity, different species properties emerged from this study that contribute to the maintenance of ground beetle functioning on various levels, even after extreme floods:

#### Being adapted to regular flooding

Extreme flood effects will be compensated by the high dispersal capacity and the high reproduction rate, hence by high re-colonization power. However, species risk complete breakdown during unpredictable floods. (Chapters two and three)

#### Being functionally equivalent

Functionally similar species risk being similarly affected during extreme floods, but this is regarded as a trade-off of maintaining functioning in an alternating ecosystem. (Chapters four and five)

#### Being habitat specialists

Although habitat specialists took longer to recover from the 2002 extreme flood, they were found to be more competitive during regular flooding and on a long-term perspective. (Chapters two and four)

This dissertation proves that floods, and in particular extreme floods, play a vital role as controlling agents of floodplains and floodplain biodiversity. They act as a re-setting mechanism for species communities, re-shape hydromorphological and hydrological conditions, and can force adaptation processes. It becomes evident from this work that extreme floods act at different response levels, causing both taxonomical and functional changes in floodplain organisms in a non-linear temporal sequence. The immediate effects can be massive, but observed on a medium-term scale or even from an evolutionary perspective, extreme floods (and even droughts) are merely a risk species bear in fluctuating, stochastic environments. For the majority of the species it is inefficient to invest in direct resistance traits, which would lower their overall fitness because less energy remains for reproduction and dispersal under regular conditions. I draw the conclusion that the breakdown of communities following extreme floods is as important as being adapted to regular floods, because after such events, biodiversity can completely rebuild the ecological networks. Some species might shift their positions within the network or the complexity of the system will change, but this could also be considered a process of adaptation of the whole network to environmental change.

Ultimately, this thesis shows that the extreme Elbe flood of 2002 had no major impacts on ground beetle composition and functioning, especially not from an evolutionary viewpoint. However, I outline that this may change if extreme events occur more frequently, given the strong connection between species adaptations and flood timing.

Investigating the effects of this event provided a deeper insight into the ways in which biodiversity recovers from extreme events, and the ecological mechanisms behind the changes, and shows the limits and the efforts required to apply ecological theory to empirical data. I strongly encourage the further development of functional approaches in biodiversity research because they can be used to explain different aspects than taxonomical approaches and can broaden our knowledge of system behavior which is hard to achieve using traditional approaches. Here, developing the applicability of the biodiversity-ecosystem functioning debate, or evaluating the relevance of neutral theory for predictive biodiversity science could be a major step forward. In this context, ecological research should focus more strongly on uncertainty, stochasticity, and non-linearity, as these aspects also emerged as major drivers in this study. Analytical methods to account for this complexity exist, but they should be adopted more frequently in ecological research. Finally, this study highlights the need to collect and analyze long-term data because this is a prerequisite to properly detect and investigate changes caused by extreme events but also gradual shifts in biological systems. Especially since transient and gradual shifts are predicted to be the main agents controlling biodiversity in the future, more effort has to be put into understanding time-lags, tipping points and thresholds of biodiversity.

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**List of Figures** *Legends are given in an abbreviated form* 

Chapter one	Fig. 1	Dyke inundation during the 2002 Elbe flood near Coswig, Germany.	10
	Fig. 2	Typical habitat mosaic of the Middle Elbe region	16
	Fig. 3	Study area and situation of the study sites in Germany	18
Chapter two	Fig. 1	Schematic approach of the randomized sampling design	24
	Fig. 2	Hydrograph of the Elbe River at gauge station Aken/Elbe.	25
	Fig. 3	Ordination of the sampling plots according to a CDA separated by sampling years.	29
	Fig. 4	Ground beetle species richness and abundances among sampling years and humidity classes.	30
Chapter three	Fig. 5	Changes in Simpson diversity and beta diversity of ground beetles.	32
	Fig. 1	Grassland habitats displaying different hydrological conditions in the study site Steckby.	48
	Fig. 2	PCA of the reduced environmental dataset.	53
	Fig. 3	Relationship between environmental variables, species occurrence, and species traits	54
	Fig. 4	Partitioning the effects of environmental variables, and species diversity on the variation of ground beetle life-history traits.	55
Chapter four	Fig. 1	Relationships between flood disturbance and different ground beetle species diversity measures based on GLMM.	74
	Fig. 2	Relationships between flood disturbance, the degree of functional simi- larity, and the richness component of ground beetle functional diversity.	76
	Fig. 3	Relationships between flood disturbance and ground beetle Functional diversity	76
Chapter five	Fig. 1	Conceptual approach to calculate functional redundancy.	94
	Fig. 2	Results of the null models to identify if the observed FR differs from random expectations.	97
	Fig. 3	Relationships between explanatory variables and functional redundancy.	98

## List of Tables

Legends are given in an abbreviated form

Chapter two	Tab. 1	Hydrological classification of the sampling plots	27
	Tab. 2	Ground beetle species richness and individual numbers	28
Chapter three	Tab. 1	Life-history traits of ground beetles used in this study.	49
	Tab. 2	Environmental variables used in the study	50
	Tab. 3	Spatial Autocorrelation based on Moran's I	52
	Tab. 4	Parameters of Procrustes rotation analysis of species and trait datasets	55
Chapter four	Tab. 1	Overview of the functional diversity indices used in this study	73
	Tab. 2	Parameters of GLMMs used to analyze the relationship between species and functional diversity and the flood disturbance	75
Chapter five	Tab. 1	Species traits used to calculate functional diversity and redundancy	92
	Tab. 2	Variables and community properties explaining ground beetle FR.	99

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#### **Publications**

- A Publications originating from this dissertation
- **Gerisch M**, Schanowski A (2009) Zur Regenerationsfähigkeit von Laufkäfern (Col., Carabidae) nach einem extremen Sommerhochwasser an der Mittleren Elbe. Naturschutz im Land Sachsen-Anhalt. *Forschung und Management im Biosphärenreservat Mittelelbe*. 46. Jg., Sonderheft 2009/1, 68-75.
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- **Gerisch, M**, Dziock, F, Schanowski, A, Ilg, C & Henle, K (2012) Community resilience following extreme disturbances: the response of ground beetles to a severere summer flood in a Central European lowland stream. *River Research and Applications*, **92**, 81-92.
- B Publications with close relation to this dissertation
- Gerisch, M, Schanowski, A, Figura, W, Gerken, B, Dziock, F & Henle, K (2006) Carabid Beetles (Coleoptera, Carabidae) as Indicators of Hydrological Site Conditions in Floodplain Grasslands. *International Review of Hydrobiology*, **91**, 326-340.
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#### C Other publications

#### ISI listed

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#### **Oral Presentations**

- 41th Annual Conference, Gesellschaft für Ökologie, Oldenburg, 05.09.2011–09.09.2011, "Can functional redundancy enhance ground beetle community stability to an extreme flood disturbance?"
- 2nd Biennial Symposium of the International Society for River Science ISRS, Berlin, 08.08.2011–12.08.2011, "Functional redundancy of alluvial ground beetles is stronger controlled by non-random trait filtering than by an extreme flood."
- 2nd Floodplain ecological Workshop (Auenökologischer Workshop), Stockstadt/Rhein, 25.03.2011–26.03.2011, "Untersuchungen zur funktionalen Redundanz von Laufkäfergemeinschaften nach einem Extremhochwasser"
- 12th Annual Conference, Gesellschaft für Angewandte Carabidologie, Schneverdingen, 2009, "Hochwasser erhöht die Artendiversität, aber nicht die funktionale Diversität von Laufkäfern in Auengrünland der Mittleren Elbe"
- 14th European Carabidologist Meeting, Westerbork, Netherlands, 14.09.2009–18.09.2009, "Suitability of ground beetles as indicator for hydrological conditions in floodplain grasslands"
- 38th Annual Conference, Gesellschaft für Ökologie, Leipzig, 15.09.2008–19.09.2008, "Variation in ground beetle traits along a gradient of flood disturbance"
- 13th European Carabidologist Meeting, Blagoevgrad, Bulgaria, 20.08.2007–24.08.2007, "Resilience capacity of riparian ground beetles after a severe summer flood on a Central European lowland stream"

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# Titel:Community resilience following extreme disturbances:<br/>the response of ground beetles to a severe summer flood<br/>in a Central European lowland stream

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