# MASTERARBEIT / MASTER’S THESIS

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## „Ant assemblages of forest and grassland in a riverine landscape in Eastern Austria are differentially impacted by flood risk“

verfasst von / submitted by

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# 1. Introduction

Ants are one of the most widespread animal families on Earth, found on all continents except Antarctica (Hölldobler & Wilson, 1990). Their wide distribution over almost all terrestrial environments is accompanied by a high species diversity and tremendous biomass. Nearly 14,000 extant ant species have been described (Bolton, 2021), but there is a general agreement among myrmecologists that the true number of species is significantly larger, with estimates up to twice that number (Lach et al., 2010; Oberprieler et al., 2018; Seifert, 2018). This high species number goes along with a high level of functional diversity in terms of ecology, allowing ants to inhabit a wide range of habitats, from deserts to tropical rainforests and even alpine regions (Lach et al., 2010). In most habitats, ants play an important role as ecosystem engineers and interact with a variety of other animal, plant and fungus species (Folgarait, 1998; Jouquet et al., 2006; Stockan & Robinson, 2016). The main characteristic uniting all ant species despite their diverse life habits is their eusociality (Hölldobler & Wilson, 1990). Ants have a reproductive division of labour and are living in colonies that vary in size from a few up to millions of individuals (Seifert, 2018). These colonies are often stationary and have a typical lifecycle, which according to Peeters and Molet (2010) can be divided in three parts: colony foundation, colony growth (production of workers) and colony reproduction (production of sexuals). For most Central European ant species, this colonial lifecycle can take up to several years to be completed (Seifert, 2018). This rather long period from colony foundation until reproduction explains why ant species can be vulnerable to habitat disturbances, especially to the ones that occur frequently enough to be likely to happen at least once during a colonial lifecycle. In temperate-zone regions, ant colonies are usually stationary, leaving them only little possibilities to avoid or escape disturbances (Andersen, 1995). Most Central European ant species build their nests close to the ground (Seifert, 2018), a trait which makes them vulnerable to habitat disturbances that effect the whole ground level like flooding and inundation events.

For some ant species, remarkably, mostly behavioral adaptations to flooding are known. For example, *Solenopsis invicta*, an invasive species in North America and beyond (Chen et al., 2020), is famous for building a raft by linking their bodies together, a technique which ensures the survival of workers, sexuals and brood in the case of inundation (Adams et al., 2011). A similar technique is used in Europe by the species *Formica selysi* and *Myrmica gallienii*. The latter one is the Central European ant species which is most adapted to flooding. In addition to being able to build rafts on the water surface, *M. gallienii* can survive flooding by either staying in sealed, solid nest types or by ascending tall plant stems (Seifert, 2018). In general, temporal or permanent relocation of the nest seems to be a common strategy for ants to survive flooding, especially in forest areas where ground-nesting species can move their nests on trees for the duration of the flood event (Adis et al., 2001; Ballinger et al., 2007; Ellis et al., 2001).

Floodplains and especially floodplain forests are rare and vulnerable ecosystems which are threatened all over the world due to intense land-use, especially agriculture, and by altered catchment hydrology (van Diggelen et al., 2006). Due to the dynamic influences on riparian areas a variety of changing microhabitats are created, which harbour a large number of animal and plant species (Ballinger et al., 2005), many of which are adapted to these dynamic environments. Regular flooding is an important factor in these ecosystems, influencing and shaping the community structure of both aquatic and terrestrial animal communities (Ballinger et al., 2005; Lasne et al., 2007; Reckendorfer et al., 2006; Vaughan et al., 2007). For terrestrial animals, inundation essentially increases mortality risks and thereby triggers local cycles of extinction and recolonization. The famous concept of the intermediate disturbance hypothesis (Connell, 1978) predicts that such disturbance regimes may contribute to elevated biodiversity, as long as frequencies or amplitudes of disturbances are not too high (Lepori & Malmqvist, 2009).

In recent years, the influence of flooding regimes on terrestrial arthropods has come more into the focus of researchers, with an increasing number of studies conducted in Central Europe (Demetz et al., 2013; Fies et al., 2016; Neumüller et al., 2018; Truxa & Fiedler, 2012). The named studies have been conducted in the Nationalpark Donau-Auen, Austria, the largest near-natural floodplain landscape in Central Europe (Fies et al., 2016). The Nationalpark Donau-Auen has been established as a study site for the influence of flooding events on terrestrial arthropod communities due to its separation into a flood-prone and a flood-protected area by a levee, which conveniently enables a comparison of arthropod communities from both areas. Regular flooding in this floodplain region is usually caused by alpine snowmelt in summer in combination with strong rainfall, increasing the water level of the Danube river which passes along the national park area (Tockner et al., 1998).

The last extreme summer flood occurred in the national park in 2013 (Blöschl et al., 2013), followed by a series of weak floods in the subsequent years (Fig.1). The summer inundation of 2020 reached the levee in some but not all parts of the national park and was not strong enough to flood the whole floodplain area between Danube and levee.

River regulation along the Danube east of Vienna in the late 19th century caused the formation of natural levees near the river banks that continuously grow since the natural side erosion and channel migration are affected and limited by the river regulation measurements (Klasz et al., 2014). Together with the riverbed degradation which is mainly caused by impoundments upstream which hold back the gravel and lead to a bed load deficit, the formation of this natural levee is causing fundamental changes in the floodplain dynamics (Reckendorfer et al., 2005). As a results of both factors, regular floods are not reaching all floodplain areas anymore and only higher discharges are able to flood the higher floodplain levels (Klasz et al., 2014). Both duration and frequency of the in inflows in the side-arms are reduced, which is leading to a decrease in their morphological dynamic (Klasz et al., 2013).

Especially in the western part of the National Park, the so-called Lobau, the sedimentation process is already far advanced, with the result that the characteristic floodplain dynamics are strongly influenced there (Reckendorfer et al., 2012).

The aforementioned studies showed that the influence of flooding regimes on arthropods differs between the species groups. While butterfly species richness declined with increasing flood impact (Fies et al., 2016), no influence on species richness could be observed for grasshoppers (Demetz et al., 2013) or moths (Truxa & Fiedler, 2012) and species richness of wild bees even increased on sites with flood impact (Neumüller et al., 2018). For all these named groups an impact of flooding regimes on the species composition was found, but the observed effects differed too much between groups to make a general statement for terrestrial arthropods.

Based on the two characteristics of Central European ants named earlier, viz. their multi-year colonial lifecycle and the stationary ground-level nests, it could be expected that most Central European ant species are more vulnerable to recurring flooding events than other terrestrial arthropods. Despite the very detailed knowledge about special adaptations of individual ant species on flooding, there is still only a limited number of studies that investigated the effect of flooding on ant species diversity and composition. Studies conducted in floodplain regions in Australia (Ballinger et al., 2007) and South America (Mertl et al., 2009) showed a decrease of species richness and change of species composition on sites with high flooding risk compared to non-flooded sites. At the same time, an increased occurrence of more opportunistic ant species was observed in the flooded areas.

Even fewer studies have been conducted on the impact of regular flooding events on Central European ants. Lude et al. (1999) found a decrease of species richness with increasing flood risk in the floodplains of an alpine river. The areas most exposed to flooding were inhabited by only a very small number of ant species, most of which had specific strategies to respond to flooding events. Glaser (2006) showed that the number of ant species inhabiting floodplain areas in Austria is quite high, with the species inhabiting floodplain areas representing 51-82% of the regional ant fauna. However, this study did not differentiate between areas with high and little inundation risk and even includes areas inside the floodplains which are not exposed to inundation, providing a refuge for species unable to tolerate floods.

The aim of this study is not only to assess how species richness and composition are influenced and shaped by recurrent flooding events, but to determine which specific life history traits are beneficial for ants to deal with inundation events. Multiple life-history traits have been described and used for analyses of ant community composition and functional diversity for Australian (Andersen, 1995) and North American (Andersen, 1997) ant species since decades. For the comparatively small Central European ant fauna, however, a similar list of life history traits has only been published recently by Seifert (2017, 2018). Nonetheless, these trait lists have already been used successfully in recent studies towards a causal understanding of variation in ant community composition along environmental gradients (Guariento & Fiedler, 2021; Scharnhorst et al., 2021).

## 1.1 Working hypotheses

My over-arching research question was how ant communities and their ecological characters are affected and shaped by recurrent, near annual summer flooding events in the Danube floodplains. I tested the following specific hypotheses:

1. Species richness and species composition change between flood-prone and non-flooded habitats, with a higher species diversity in non-flooded habitats.
2. The effect of flooding on species richness is higher in grassland than in forest habitats, as trees might serve as a refugial area, and dead wood might offer additional protection against (short term) inundations.
3. Functional trait diversity and trait composition change with ant species composition along the environmental gradient of being exposed to flooding, indicating which traits might be beneficial for ants to survive in flooded areas.

# 2. Material and Methods

## 2.1 Study area

The study was conducted in the Nationalpark Donau-Auen, Austria, which extends from the eastern border of Vienna along the Danube river to the Slovakian state border near Bratislava. With a length of over 38 km, the national park represents the largest contiguous, near-natural floodplain landscape in Central Europe (Fies et al., 2016). The Nationalpark Donau-Auen was legally established in 1996 and is recognized by the IUCN as a category II reserve. The current national park area covers over 9,600 ha, which consist of 65% floodplain forest and 15% meadows, while 20% are permanently covered by water (Nationalpark Donau-Auen GmbH, 2021). Fluctuations in the water level of the Danube, which still has the character of a mountain river in the national park area, cause near annual summer flooding events between June and August (Blöschl et al., 2013). A flood protection dam built in the 19th century ("Marchfeldschutzdamm") north of the Danube divides the national park into two parts. The protection dam, going from east to west, cuts the national park area in a northern and a southern part. Only the southern section between the Danube and the levee is still affected by inundation typical for the floodplain, while the area north of the dam has not been subject to the regular flooding regime since about the 1870ies (Klasz et al., 2014).

This division of the national park area has a clear influence on the vegetation. Only on the southern side of the dam, the true riparian forest with the characteristic softwood trees and gravel plains can still be found. In the northern part, where flooding dynamics are only caused by high ground-water levels, the main vegetation today consists increasingly of hardwood forests. These forests have also been shaped by reforestation efforts and silvicultural management up until the 1990s (Nationalpark Donau-Auen GmbH, 2021).

Next to the forest, the second main terrestrial habitat type in the park area are meadows, which were established centuries ago for agricultural usage. Nowadays, the agricultural usage and management is limited to mowing once or twice a year to keep the landscape-shaping element open and maintain the quality of the meadows as sites that harbour many organisms of conservation concern.

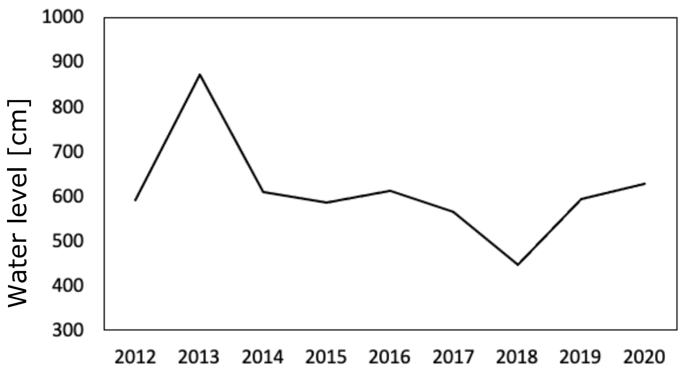

*Figure 1.* Maximum water levels of the Danube river at Wildungsmauer (Lower Austria) during the summer months between May and September from the years 2012 to 2020 (Data from DoRIS 2021).

## 2.2 Study sites

Ant sampling was conducted on 32 sites in the Nationalpark Donau-Auen. The 32 sampling sites consisted evenly of the two dominating habitat types of the national park, viz. riparian forests and meadows, as different ant species were expected to thrive in these habitats. Half of the sampling sites were selected north of the levee and were thus not exposed to the flooding regime. The other half of the sampling sites was situated south of the levee, in areas which are still exposed to more or less regular flooding events (Fig. 2).

These 32 selected sites were classified according to their habitat type and location relative to the dam as following: “forest north”, “forest south”, “grassland north” and “grassland south”.

The individual sites of each habitat type have been numbered from 1 to 8 and are referred to as "forest north 1", "forest north 2",…,"forest north 8" or abbreviated as "FN1", "FN2",...,"FN8". The abbreviations for forest south, grassland north and grassland south are FS, GN and GS respectively. (Fig. 2, Tab. 1).

To ensure quick access to all sites, the sample locations were not distributed throughout the whole national park area, but in the central area of the national park, close to the villages of Orth and Stopfenreuth, respectively. 16 sampling sites were selected near each village, consisting of four representatives of each of the above-named categories.

Sampling sites were defined as 100°m$^2$ of homogenous habitat (10x10°m). The minimum distance between sampling sites of the same habitat type was 300 m to ensure spatial independence.

All sampling sites were chosen in a way that they represented a gradient of the different vegetation types of both forest (hardwood and softwood) and meadows. The selection of the exact sites (Fig. 2) was based on vegetation data provided by the national park administration and the ÖBf (Österreichische Bundesforste – Austrian Federal Forest Office).

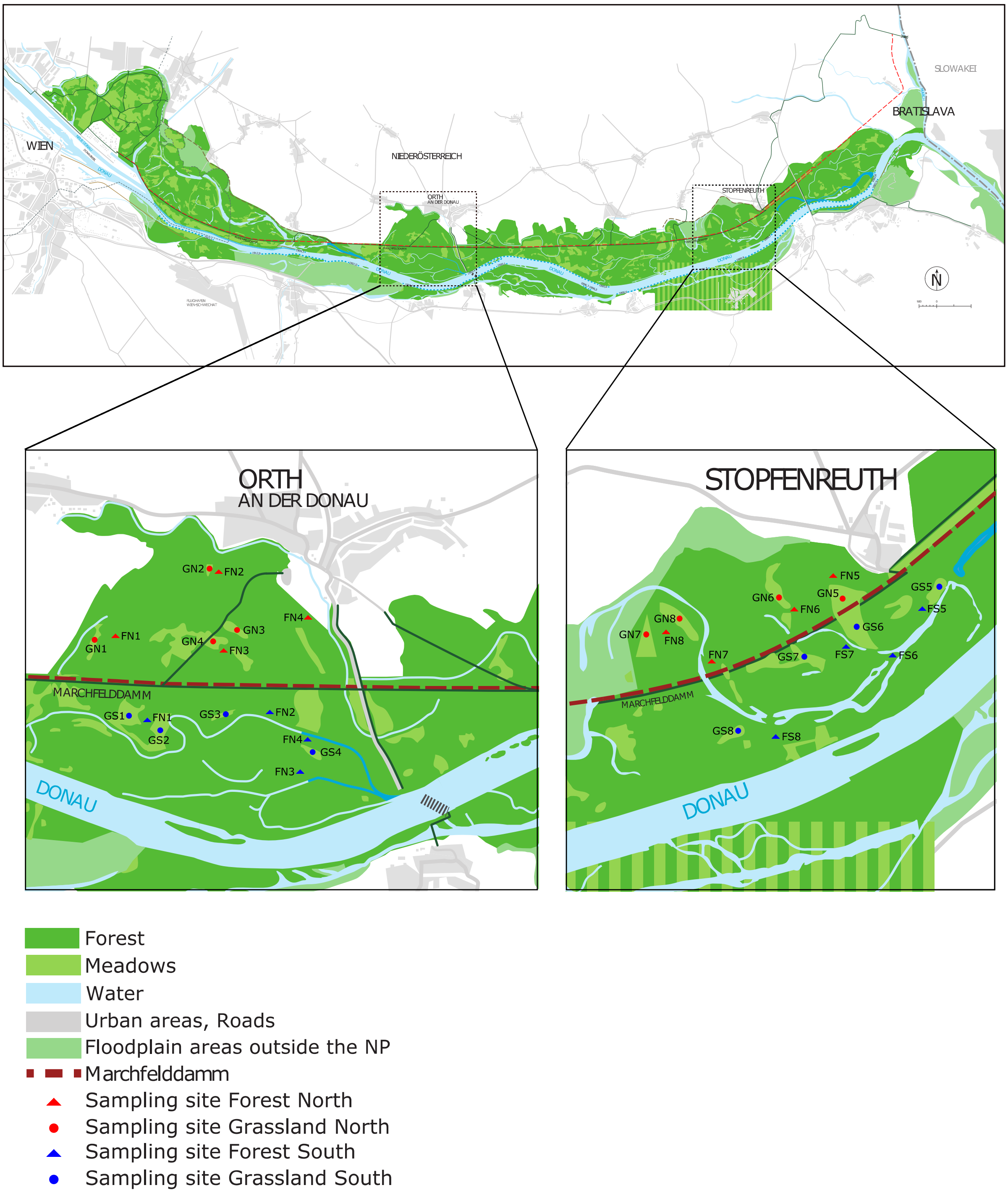

*Figure 2.* Map of the Nationalpark Donau-Auen with enlargement of the two study areas close to Orth and Stopfenreuth. The 32 sample sites are marked in the enlargement. The basic map was kindly provided by the Nationalpark and adapted to show the sampling sites.

## 2.3 Field sampling

Applying a combination of different methodologies and approaches can result in a more complete inventory of ant species than by relying on a single sampling method (Delabie et al., 2000; Hunter, 2001). To reach a near-complete inventory of all ant species in a given habitat often a combination of numerous methodologies has to be used, as listed in the ALL protocol (Agosti & Alonso, 2000). However, the time and effort to obtain a complete inventory of all different ant species in the national park area would have been disproportionate to the research questions of this study. In order to obtain a reasonable combination of sampling effort and faunal coverage, I therefore accepted that some rare species, especially socially parasitic species living as inquilines or strictly arboreal ant species were unlikely to be sampled with the methods used.

Next to the aim of the study, the type of habitat to be studied is particularly important for the selection of methods. Following the evaluation for sampling of ants by Tista and Fiedler (2011), a combination of pitfall traps and Winkler litter extraction was finally chosen for this survey.

Pitfall traps are a very commonly used technique to collect ants and yield the best results in species numbers in many studies in the temperate region (Arnan et al., 2006). However, the exclusive use of pitfall traps means that some species may not be recorded at all, especially arboreal and hypogaeic species (Tista & Fiedler, 2011).

Since this study focuses primarily on ground-dwelling ants, the selection of collection methods neglected a targeted survey of arboreal ants. To expand the sampling of ant species to include hypogaeic species, Winkler litter extraction was selected as the second sampling method. This method is often used complementary with pitfall traps and the combination of both methods shows good results in catching both larger and active as well as smaller, less active ant species (Olson, 1991; Silva et al., 2013).

### 2.3.1 Pitfall traps

Pitfall traps are commonly used for surveying ground dwelling ant communities (Bestelmeyer et al., 2000; Tista & Fiedler, 2011). With this method, the abundance and species composition of ground-surface active ants can be estimated (Bestelmeyer et al., 2000). Exposition time of the pitfall traps and the number of traps can be reduced when using a baiting liquid instead of a plain killing agent (Schlick-Steiner & Steiner, 1999).

Five pitfall traps (plastic cups, height 9.9 cm, diameter 7 cm) were placed at each sampling site with at least 3 meters distance from another and from the sites of litter samples collected for the Winkler extraction (Fig. 3). The baiting liquid used was a mixture of rum and honey (1:1) with a few drops of detergent to reduce surface tension, as used in Tista and Fiedler (2011). The plastic cups were filled up to ¼ of the cup size (ca. 0,05l) with the baiting liquid. Traps were placed in a way that the trap edge was on the same level as the soil surface. To keep larger animals away from the traps, these were covered with wire grid (mesh size 1 mm). A plastic roof was placed over the buried pitfall traps as rain protection. All pitfall traps were placed at each sample site for 72 h, after which samples were collected, washed, and transferred to 70% ethanol. Each pitfall trap was counted as a single sampling unit, and the sampled individuals from each pitfall trap were stored and processed separately from other ant individuals collected at the same site.

### 2.3.2 Winkler litter extraction

While pitfall traps proved to deliver good results in sampling ground-active ant species, they are not effective when it comes to hypogaeic ant species (Majer, 1997). Best results in sampling litter-dwelling and hypogaeic species are achieved by the Winkler extraction method (Bestelmeyer et al., 2000).

For the Winkler extraction, all leave and grass litter from a 1°m$^2$ area of ground was sifted manually with a wire mesh (1 cm mesh width). On each sampling site, three locations were randomly selected for the litter collection, with at least 3 m distance to the nearest Winkler sampling location or pitfall trap (Fig. 3). The sifted litter was then put in a plastic bag and transported to a laboratory at the Department of Botany and Biodiversity Research of the University of Vienna. In the laboratory, the collected litter was placed in the inner nets of the Winkler bags (6mm mesh width) and remained there hanging for 72 h. Details of constructions of Winkler bags are described in Bestelmeyer et al. (2000). The Winkler bags were sealed at the top end, and a cup containing 70% ethanol was attached to the bottom end to collect falling ants. After three days the cups with the collected ants were retrieved and the sampled ants were stored for identification. Similar to the pitfall traps, each collected litter ant sample was counted as a distinct sampling unit and the retrieved ants of each litter sample were not mixed with other samples from the same site.

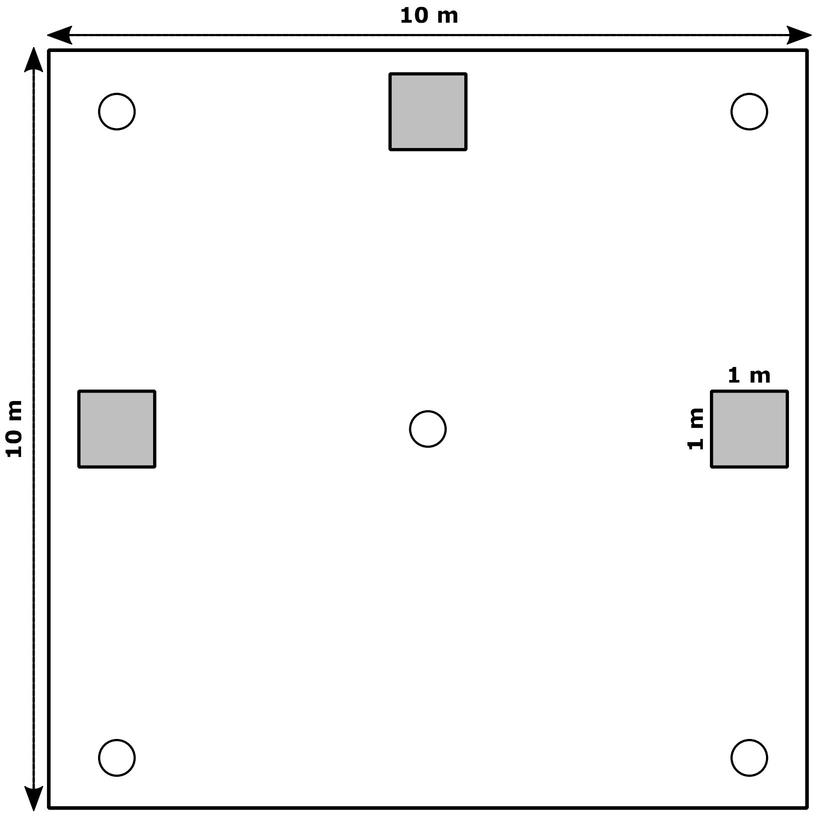

*Figure 3.* Scheme of a sampling plot. The white circles indicate the positions of the pitfall traps, the grey boxes indicate the positions where the litter was collected for the Winkler extraction. The distance between all taken samples in a plot was at least three meters to avoid oversampling an ant species if traps/the litter sampling was placed close to a nest.

### 2.3.3 Sampling period

Two rounds of sampling were conducted on each site, resulting in ten pitfall trap samples and six litter samples per site, adding up to 512 samples over all sites and the whole sampling period. The first round of sampling was conducted from June-July 2020, the second round from July-August with an interval of a month between the two sampling rounds at each site.

### 2.3.4 Habitat characters

Several habitat variables were recorded to place the ant surveys in an environmental context and to quantify differences more objectively between habitats and test their specific influence on the occurrence of individual ant species. The following variables were recorded: geographic position, altitude (both measured with a Garmin GPS device), canopy cover, litter coverage, litter depth, and grass coverage. To estimate canopy coverage, five digital photographs were taken in vertical direction at each sampling site in all forest habitats, from approximately one meter above ground. The photographs were taken from each pitfall trap location, to ensure a distribution over the whole sampling site. The pictures were then converted to black and white images, using an image-processing software (Image J version 1.53a). The arithmetic mean of the fractions of black pixels obtained from the five images was used for subsequent analyses.

Litter coverage and grass coverage was scored at each site by visually estimating the percentage of litter/grass coverage on five spots with a size of 1m$^2$. The mean of the values obtained from these five spots was used for subsequent analyses.

Litter depth was measured by inserting a long nail in the litter and marking the top of the litter layer on the nail. This was done at five random spots at each site and again the mean of the values obtained from these five spots was used for subsequent analyses.

## 2.4. Species identification

The identification of all sampled ants took place from September 2020 to January 2021 at the Department of Botany and Biodiversity Research of the University of Vienna. Ant voucher specimen collected were determined morphologically to species level using the keys of Seifert (2018) and Wagner et al. (2017) with the help of a stereo-microscope (90-fold magnification). Measurements under the microscope were done with the software Motic Images Plus 3.0. DNA-barcoding of voucher specimens of the genus *Tetramorium* was performed at the University of Vienna by Dr. Brigitte Gottsberger, using the standard laboratory protocol for the barcoding fraction of the mitochondrial cytochrome oxidase I (COI) gene of the Analytik Jena innuPREP DNA Micro Kit (https://www.analytik-jena.de/). Used modifications of this protocol are as listed in Gottsberger et al. (2021) with the only difference that a destructive DNA extraction was used that lead to the destruction of either a leg or the whole ant specimens.

## 2.5. Ant species traits

Thirteen different life-history traits of all observed ant species where selected to evaluate how the functional trait diversity and trait composition may change along the environmental gradient of exposition to inundation. The traits could be organized in four categories: colony and nest related traits (mean colony size, maximum colony size, number of queens per colony, number of nests per colony, and nest position), feeding related traits (foraging stratum, recruitment behavior and contribution of trophobiosis to diet), morphology and dominance related traits (mean body size of worker and position in dominance hierarchy), and reproduction related traits (colony foundation type, overwintering with brood, mean swarming period of winged gynes).

Information for the selected traits was taken from Seifert (2017); (2018) and Arnan et al. (2017). In the few cases, where no information for a specific trait for a species could be found or where the traits states were unknown, the trait characteristics from the closest related ant species found in this study was used. For example, no exact information on the contribution of trophobiosis to the diet of *Tetramorium immigrans* and *T. staerckei* could be found, so the values for *T. caespitum* were used in that case. These extrapolated values were marked in the trait matrix (Table S2 in Appendix).

## 2.6. Statistical methods

The data set for all statistical analyses was compiled as a species x site incidence (or pseudo-abundance) matrix. Incidence data was chosen instead of sums of individuals because ants, as social insects have the problem of extreme spatial clumping of individuals within samples (Longino et al., 2002). Since each site was represented by 16 sampling units (ten pitfall traps and six Winkler extractions), the highest possible incidence score of a species per site was 16. These incidence scores, which aggregated the results from the two sampling rounds, served as a metric of pseudo-abundance (or prevalence) of each ant species at every site.

### 2.6.1 Species richness and accumulation curves

Sampling coverage and species accumulation was analyzed in iNEXT Online ((Chao et al., 2016) with the species incidences of all sixteen sampling units per site serving as pseudo-abundance. All other analyses were performed in the program PAST 4.04 (Hammer et al., 2001). Observed species richness per site was analyzed by a two-way ANOVA with the habitat type (forest/grassland) and exposition to flooding (yes/no) as main factors.

### 2.6.2 Community composition

Community composition and its drivers were analyzed with both constrained and unconstrained ordinations. A non-metric multidimensional scaling (NMDS) analysis was performed based on the incidence matrix. The Bray Curtis index was always used as similarity index. This unconstrained ordination method uses rank orders and allows extracting structures out of multidimensional relationships between samples and to ordinate those samples in a low-dimensional space (Kindt & Coe, 2005). To test if the two sampling methods showed different results in the community composition, ant species lists derived from both methods were analyzed separately in the NMDS.

A two-way PERMANOVA with 10,000 permutations was performed to test whether species composition differed significantly between habitat types and exposition to flood risk.

For constrained ordination, a canonical correspondence analysis (CCA) was performed to place the community composition in context with the following environmental variables: canopy cover, litter coverage, litter depth, grass coverage and flood risk. The environmental data was z-transformed prior to the analyses to allow comparisons on the same scale. Prior to the z-transformation, all data given in fractions were logit-transformed according to Warton and Hui (2011).

Next to clusters of sites with similar species composition and vectors indicating the influence of environmental variables on these clusters, a CCA allows to visualize the position of individual species in the ordination diagram (Ter Braak & Verdonschot, 1995).

### 2.6.3 Species traits and community weighted means

The values of the thirteen selected trait species were scored in different scales. For the mean worker body size (in mm) and the mean and maximum colony size continuous numbers were used. The values for mean and maximum colony size were log-transformed prior to further analyses to ensure homogeneity of variances. Following five traits were measured on an ordinal scale: number of queens per colony (0: strictly monogynous, 0.5: facultatively polygynous, 1: usually polygynous), number of nests per colony (0: monodomous, 0.5: facultatively polydomous, 1: usually polydomous), colony foundation type (0: independent colony foundation, 0.5: independent and dependent colony foundation, 1: dependent colony foundation), foraging stratum (0: strictly on ground, 0.5: ground and arboreal, 1: arboreal foraging predominant) and type of foraging (0: foraging individually, 0.5: group recruitment, 1: mass recruitment). The following three traits were measured on a binary scale: nest position (0: nest in/on ground layer, 1: nest at least sometimes arboreal, above ground layer); overwintering with brood (0: no, 1: yes); and position in dominance hierarchy (0: subdominant species, 1: dominant and territorial species). The importance of trophobiosis in diet was given in fractions, and the mean date of the swarming period of gynes was noted as day of the year [1-365].

To create the community weighted means matrix, the values of the single traits were weighted according to the pseudo-abundances at the sampling site and then divided by the total number of incidences at this site.

A two-way ANOVA was performed for each of the thirteen selected traits with habitat (forest/grassland) and flood risk (yes/no) as main factors. In case of a significant interaction effect, a Tukey's post-hoc test was applied to localize effects. The distribution of each trait per site was visualized in a boxplot.

To put the community weighted means in context with the community composition, a principal components analysis (PCA) was performed based on the community weighted means matrix. Prior to creating the PCA, all data given in fractions was logit-transformed according to Warton and Hui (2011). Subsequently, all data was z-transformed.

# 3. Results

## 3.1 Ant species observed and species richness

During the survey, a total number of ~35,500 ants were collected and identified, representing 28 different species (Tab. 1). Nine of the observed species are listed in the red list of endangered species for Lower Austria (Schlick-Steiner et al., 2003).

*Table 1.* Ant species found on the 32 sites in the Danube floodplain near Orth and Stopfenreuth. Sites are sorted according to the four habitat types (red=northern sites, blue=southern sites).

| | **Sampling Site** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Forest North** | | | | | | | | **Forest South** | | | | | | | | **Grassland North** | | | | | | | | **Grassland South** | | | | | | | | |
| **Species** | FN1 | FN2 | FN3 | FN4 | FN5 | FN6 | FN7 | FN8 | FS1 | FS2 | FS3 | FS4 | FS5 | FS6 | FS7 | FS8 | GN1 | GN2 | GN3 | GN4 | GN5 | GN6 | GN7 | GN8 | GS1 | GS2 | GS3 | GS4 | GS5 | GS6 | GS7 | GS8 | **Nr. Sites** |
| *Camponotus fallax* (Nylander, 1856) | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Dolichoderus quadripunctatus* (Linnaeus, 1771) | | | X | | | X | | | | | | | X | X | | | | | | | | | | | | | | | | | | | 4 |
| *Formica cunicularia* Latreille, 1798 | | | | | | | | | | | | | | | | | X | X | X | | X | X | X | X | | | | | X | X | X | X | 11 |
| *Formica rufibarbis* Fabricius, 1793 | | | | | X | | | | | | | | | | | | | | X | | X | X | X | X | X | | | | X | X | | | 9 |
| *Formica sanguinea* Latreille, 1798 | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | | | | 1 |
| *Lasius brunneus* (Latreille, 1798) | | | | | X | | | | | | | | | X | | | | | | | | | | | | | | | | | | | 2 |
| *Lasius emarginatus* (Olivier, 1792) | | | | X | | | | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | 5 |
| *Lasius flavus* (Fabricius, 1782) | | | | | X | | | | | | | | | | X | | | | | | | X | | | | | | | | | | | 3 |
| *Lasius fuliginosus* (Latreille, 1798) | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Lasius niger* (Linnaeus, 1758) | | | | | | | | | | | | | | | | | X | X | | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| *Lasius paralienus* Seifert, 1992 | | | | | | | | | | | | | | | | | | | X | | | | | | | | | | | | | | 1 |
| *Lasius platythorax* Seifert, 1991 | X | X | X | | X | X | X | X | X | X | X | X | X | X | X | X | | | | | | | | | | | | | | | | | 15 |
| *Leptothorax gredleri* Mayr, 1855 | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | 1 |
| *Myrmecina graminicola* (Latreille, 1802) | X | X | X | X | X | X | | | | | | | X | | | | | X | | | | | | | | | | | | | | | 8 |
| *Myrmica rubra* (Linnaeus, 1758) | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X | | | | | | | | | | | X | | 19 |
| *Myrmica ruginodis* Nylander, 1846 | | | X | | | | | | | | | | X | | | | | X | | | | | | | | | | | | | | | 3 |
| *Myrmica sabuleti* Meinert, 1861 | | | | | | | | X | | | | | | | | | X | X | | X | X | | X | X | | | | | | | | | 7 |
| *Myrmica schencki* Viereck, 1903 | | | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | | 1 |
| *Ponera coarctata* (Latreille, 1802) | X | | X | | X | X | X | X | | | | | | | X | X | | X | | | | | | | | | | | | | | | 9 |
| *Ponera testacea* Emery, 1895 | | | | | | | | | | | | | | | | | | X | | | | | | | | | | | | | | | 1 |
| *Solenopsis fugax* (Latreille, 1798) | | | | | | | | | | | | | | X | | X | X | X | X | | X | X | X | X | X | X | | X | X | X | X | X | 16 |
| *Stenamma debile* (Foerster, 1850) | X | X | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Tapinoma erraticum* (Latreille, 1798) | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | | | | 1 |
| *Tapinoma subboreale* Seifert, 2011 | | | | | | | | | | | | | | | | | | X | X | | X | | X | X | | | | | | | | | 5 |
| *Temnothorax crassispinus* (Karavajev, 1926) | X | X | X | X | X | X | X | X | X | X | | X | X | X | X | X | | | | | | | | | | | | | X | X | | | 17 |
| *Tetramorium caespitum* (Linnaeus, 1758) | | | | | | | | | | | | | | | | | | | X | | X | X | X | X | | | | | | | | | 5 |
| *Tetramorium immigrans* Santschi, 1927 | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | 1 |
| *Tetramorium staerckei* Kratochvil, 1944 | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | | | | | 1 |
| **Nr. Species per site** | 8 | 5 | 8 | 4 | 8 | 6 | 4 | 5 | 3 | 3 | 2 | 5 | 7 | 7 | 6 | 5 | 5 | 9 | 6 | 3 | 7 | 6 | 8 | 9 | 3 | 3 | 1 | 3 | 5 | 5 | 4 | 3 | |

The highest species richness (Fig. 4, Tab. 2) was found at the northern grassland sites with up to 9 different species at the same sample site. The lowest species richness was found in the southern grassland sites where the maximum species number on a sampling plot was five, and on one site only one single ant species was observed.

*Table 2.* Results of a two-way ANOVA on ant species richness across the habitat types (forest/grassland) and flood risk (yes/no). *: significant at $p < 0.05$

| | Sum of squares | Degrees of freedom | Mean square | F | p |
|---|---|---|---|---|---|
| **Habitat** | 0.78 | 1 | 0.78 | 0.23 | 0.63 |
| **Flood Risk** | 38.28 | 1 | 38.28 | 11.48 | <0.01* |
| **Interaction** | 7.03 | 1 | 7.03 | 2.11 | 0.16 |
| **Within** | 93.38 | 28 | 3.34 | | |
| **Total** | 139.47 | 31 | | | |

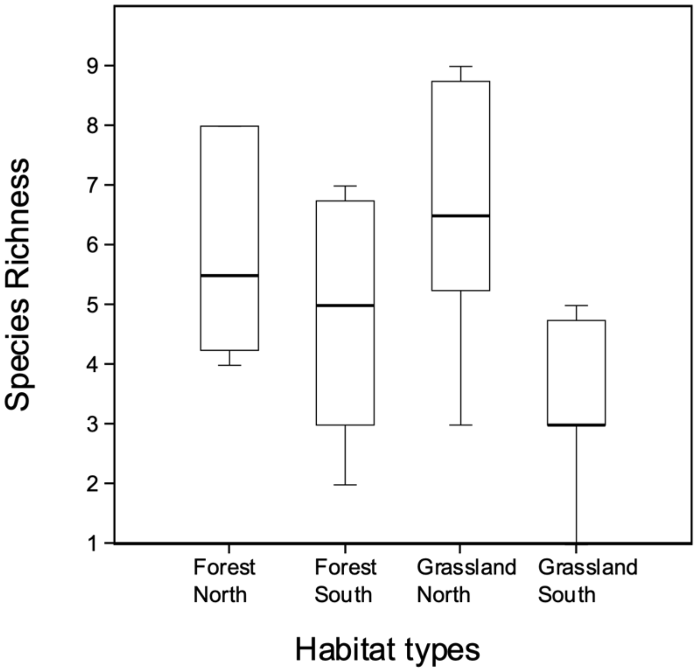

*Figure 4.* Boxplot of ant species richness across the four habitat types. Whiskers show the range of observed data, the boxes depict the inter-quartile ranges, and the line showing the median. The median species number at the northern grassland sites was the highest with 6.5 species per sampling site, while the median of species number found was lowest in the southern grassland with only 3 species.

Flood risk had a significant effect on ant species richness (Tab. 2). This effect could be observed in comparison of the two grassland habitat types, which had the highest (northern grassland) and the lowest (southern grassland) species numbers of the four habitats. The same effect of flood risk could not be observed in the forest habitats, where the northern sites only had a slightly higher median of species number per site (Fig. 4).

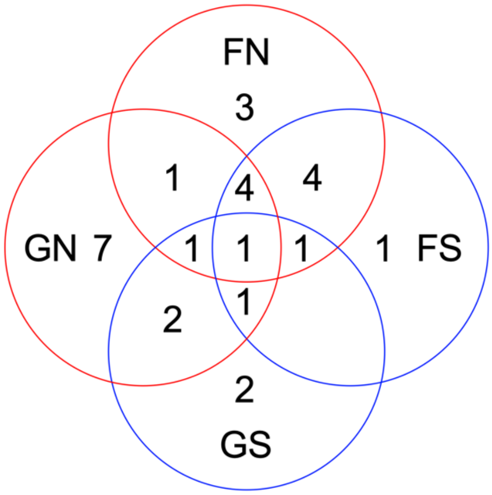

*Figure 5.* Venn diagram of the occurrence of ant species in the four habitats (FN: forest north; FS: forest south; GS: grassland south; GN: grassland north). No single ant species was found to occur only in a combination of Grassland North – Forest South or Forest North – Grassland South.

*Myrmica rubra* was the overall most abundant and only ant species that was found through all four habitats. Eight ant species were exclusively found in forest habitats, while nine species were exclusive for the meadows. Just three species were found only on the southern sampling sites, contrasting to the large number of eleven species only found in the non-flooded, northern parts. Out of these eleven, seven species were exclusively found in the northern grassland (Fig. 5).

Following *M. rubra* as the most abundant species (found at 19 sites), *Temnothorax crassispinus* (17 sites), *Solenopsis fugax (*16 Sites), *Lasius niger* and *Lasius platythorax* (both at 15 sites) were the most sampled species. Both of these *Lasius* species covered nearly all sampling sites of their specific habitat, with *L. niger* occurring on 15 of the 16 grassland sites, and *L. platythorax* being found on 15 of the 16 forest sites.

Nine of the 28 identified species, viz. *Camponotus fallax, Formica sanguinea, Lasius fuliginosus, Lasius paralienus, Leptothorax gredleri, Ponera testacea, Tapinoma erraticum, Tetramorium immigrans* and *Tetramorium staerckei* were only found on one single site each.

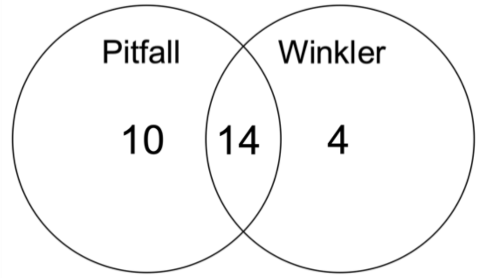

*Figure 6.* Venn diagram of the ant species captured with the two different sampling methods. Half of all observed species were captured by both methods. Only four species were captured exclusively with the Winkler extraction, while 24 of the 28 observed species were collected in pitfall traps.

Comparing the sampling methods, the pitfall traps showed to be more productive in species numbers than the Winkler extraction (Fig. 6). 24 of all collected species were found in the pitfall traps, while only the four species *Myrmica schencki*, *Ponera testacea*, *Stenamma debile* and *Tetramorium immigrans* were found exclusively in Winkler samples.

A species accumulation curve was computed to estimate the total species richness in the sampling area and to evaluate how complete the sampling of the ant species was. For both southern habitat types a very high coverage of ant species was reached, and a higher number of sampling units would most likely only contribute one or two additional species, if at all. For both northern habitat types, in contrast, a higher number of sampling units would have potentially increased the number of species found (Fig. 7).

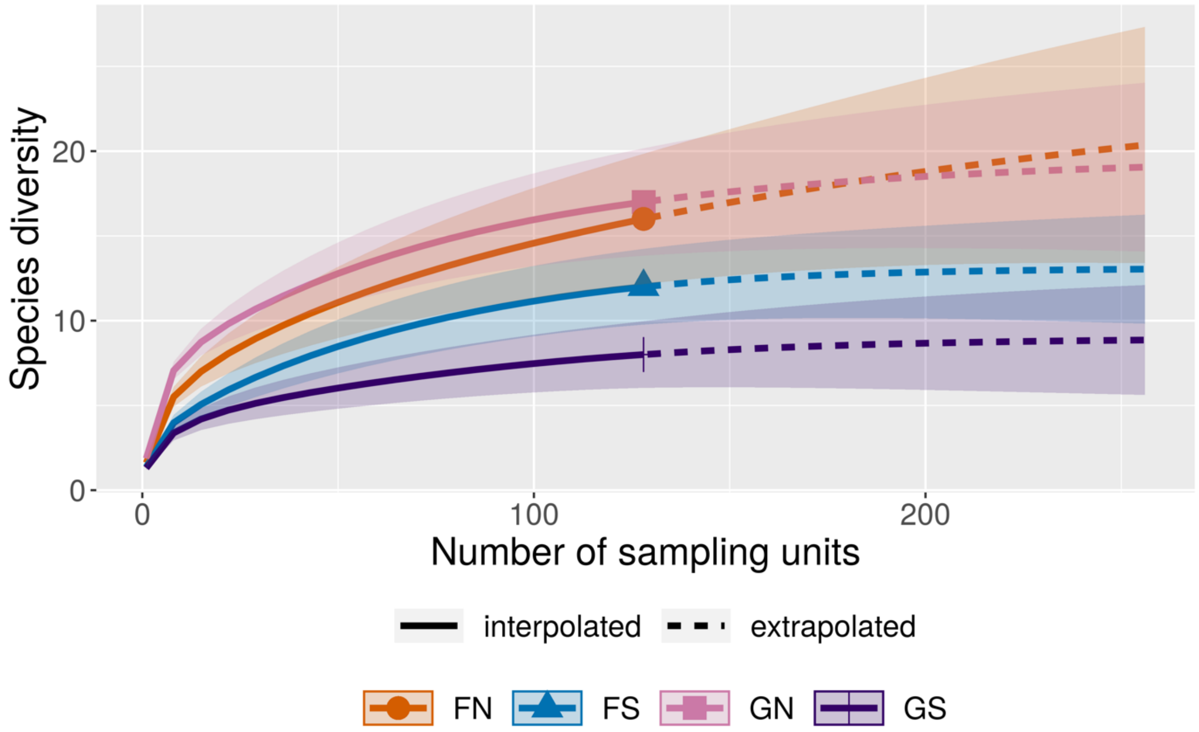

*Figure 7.* Sample-size-based rarefaction and extrapolation curves for the four habitat types, based on species incidences. Beta diversity was higher among the northern sites, here a few ant species have likely been missed.

### 3.2 Species composition of ant communities

The community composition of the ant species between all sites was analyzed using relative species (pseudo-)abundances. To get a first impression of how the ant communities differed between the habitat types, an unconstrained ordination (NMDS) was computed (Fig. 8 and Fig. 9).

The aim of these ordinations was mainly to visualize how habitat and flood risk are shaping community composition. Additionally, to find out whether the different sampling methods cover different fractions of the ant community, the results obtained with the two sampling methods were presented separately for each site.

In Fig. 8, a clear separation of the ant assemblages of the forest and the meadow habitats is apparent. Overall, the clusters also show a clear signature of the sampling method. In the forest habitats, the ant assemblages sampled with pitfall traps from the northern sites were nearly completely overlapping with the assemblages sampled with pitfall traps from the southern sites.

The pitfall traps placed in the forest habitats showed to capture very similar ant species, which is shown by the overlap of the ant assemblages from northern and southern sites.

In contrast, the ant assemblages in the forest habitats sampled with the Winkler method from both habitat types were not overlapping at all. This indicates that flood events in the forest habitats have an influence on shaping the community of ant species living in the leaf litter, while the more active ant species, which are usually captured by pitfall traps, are less affected.

In the meadow habitats, a bigger overlap regarding the clusters of the different sampling techniques was observed. The overlap of the ant assemblages of the northern Winkler samples with both groups of pitfall samples was caused by one sampling site where only a single ant species was recorded in all Winkler samples (Site-ID: GN4). In Fig. 9 this site is represented by the red, non-filled circle which is closest to the x-axis. When excluding this site from the ordination plot (Fig. 9), a clear separation between the two sampling methods emerged for the meadow habitats, just like the separation seen among the forest habitats.

As observed in the forest habitats, pitfall and Winkler samples of the meadow habitats captured different parts of the ant community. While for both sampling methods a small overlap of northern and southern sampling sites was noticeable, no clusters were as similar to each other like the forest pitfall clusters. This shows that the complete ant community of the meadows is influenced and shaped by flooding events and not only the litter inhabiting ant species, as in the forest habitats.

A two-way PERMANOVA was performed to test if the ant clusters visualized in the ordination diagrams also differed significantly from each other depending on habitat type and flood risk. Significant results were obtained for both predictors (Tab. 3).

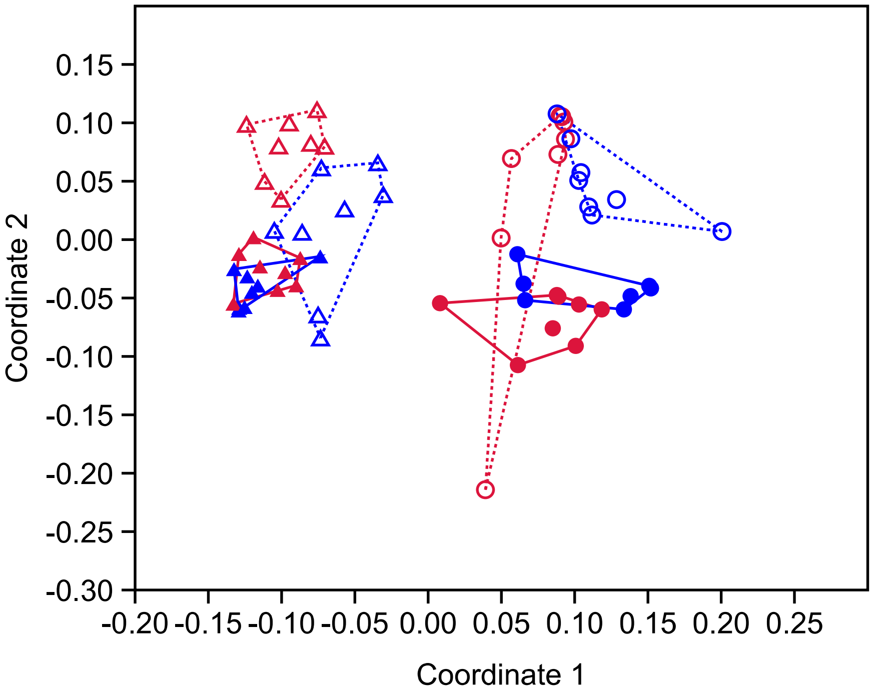

*Figure 8.* NMDS plot (stress: 0.31) of the ant assemblages across all sampling locations, based on Bray-Curtis similarities. Colours indicate the position of the sampling sites relative to the levee (blue = south, red = north of the levee), symbol shapes indicate the habitat types (triangle = forest, circle = grassland) and filling indicates the sampling method (filled = pitfall, empty =Winkler). The clusters of ant assemblages are not only depending on the habitat type and flood risk, but also on the sampling method.

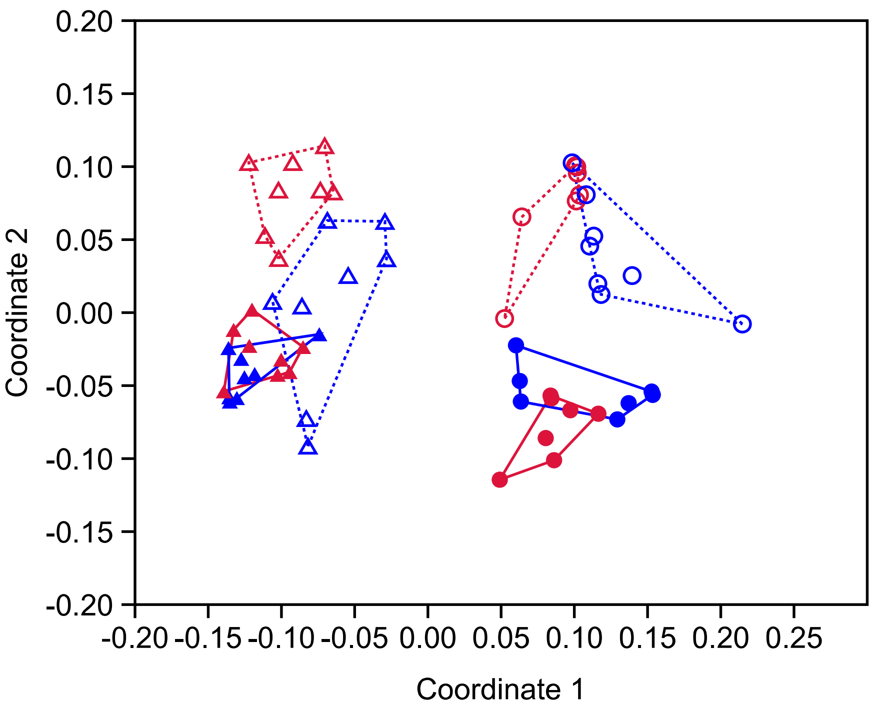

*Figure 9.* NMDS plot (stress: 0.31) of the ant assemblages across all sampling locations without the results from the Winkler extraction from site GN4. Symbols as in Fig. 7. After excluding this sample where only a single species was found by the Winkler method, a clearer clustering of the separate survey methods can be observed also for the grassland habitats.

*Table 3.* Results of a two-way PERMANOVA on ant community composition, based on Bray-Curtis similarities (10000 permutations). *: significant at p < 0.05.

| Source | Sum of squares | Degrees of freedom | Mean square | F | p |
|---|---|---|---|---|---|
| **Habitat** | 8.25 | 1 | 8.25 | 39.85 | <0.01* |
| **Flood Risk** | 0.76 | 1 | 0.76 | 3.68 | <0.01* |
| **Interaction** | 0.78 | 1 | 0.78 | 3.76 | <0.01* |
| **Residual** | 12.42 | 60 | 0.21 | | |
| **Total** | 22.21 | 63 | | | |

A canonical correspondence analysis (CCA) was performed as a constrained ordination to put the 28 species and five environmental variables in context with the ant community composition (Tab. 4; Fig. 10). A strong segregation of the forest and grassland habitats was observed, which is underlined by the long vectors of canopy density, litter density and grass coverage. Litter coverage had only a very minor influence on the ordination outcome and seems to be irrelevant for the observed ant species. The vector for flood risk was much shorter compared to the first three named vectors, demonstrating that the habitat type had a bigger influence on ant species composition than the potential risk of flooding events per se. Nonetheless a gradient of the individual ant species was observed in the meadow habitats along the flood risk vector, indicating which species are particularly sensitive to flood risk. No similar dispersion along the flood risk gradient was observed for the ant species connected to the forest habitat, corroborating that the effect of inundation on ant communities was a lot smaller in forests than on grassland habitats. Both axes in the CCA ordination contributed significantly to the segregation of ant assemblages (Tab. 4).

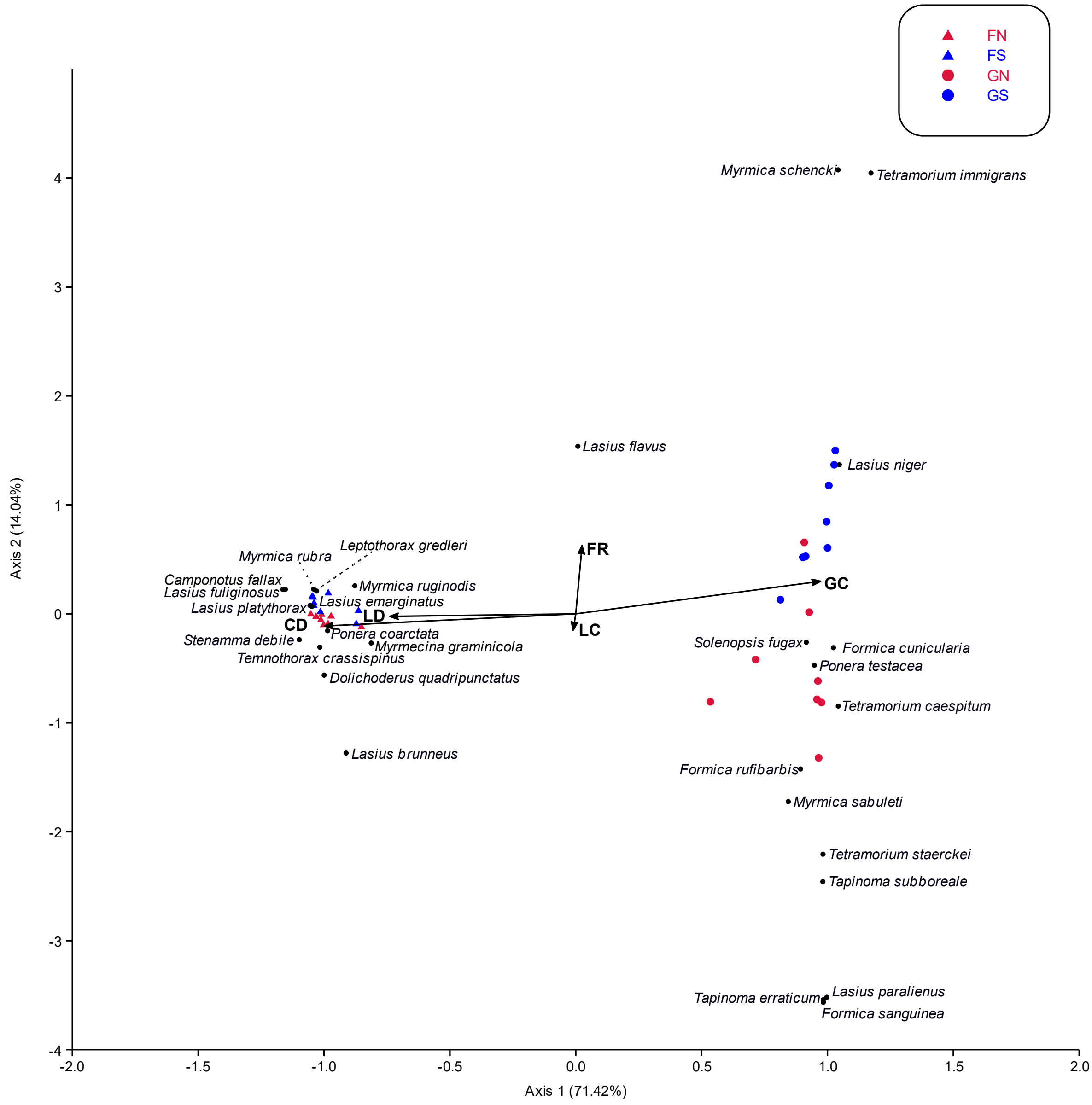

*Figure 10.* CCA ordination plot of the observed ant assemblages and species, showing how ant community composition is influenced by five environmental variables (CD = canopy density; LD = litter density; LC = litter coverage; GC = grass coverage; FR = flood risk). Colours indicate the position of the sampling sites relative to the levee (blue = south, red = north of the levee), symbol shapes indicate the habitat types (triangle = forest, circle = grassland) Arrows indicate the correlation of the respective variable with the community composition. All observed ant species are included in this ordination. Values on the axis refer to the percentage of Eigenvalues. Symbols have been moved slightly for visual clarity to reduce overlap.

*Table 4.* Results of a permutation test on both canonical axis of the CCA ordination (9999 permutations). The trace value of the community matrix was 1.26, with a p value of 0.0001. *: significant at p < 0.05.

| Axis | Eigenvalue | P |
|---|---|---|
| **1** | 0.9 | <0.01* |
| **2** | 0.18 | <0.01* |

## 3.3 Community weighted means of species traits

Community weighted means of traits were calculated for 13 species traits which were assorted into four groups (colony related traits, feeding related traits, morphology and dominance related traits and reproduction related traits; Figs. 11-14). For each trait, a two-way ANOVA was performed to test if the observed differences between the four habitat types were significant (Tab. 5).

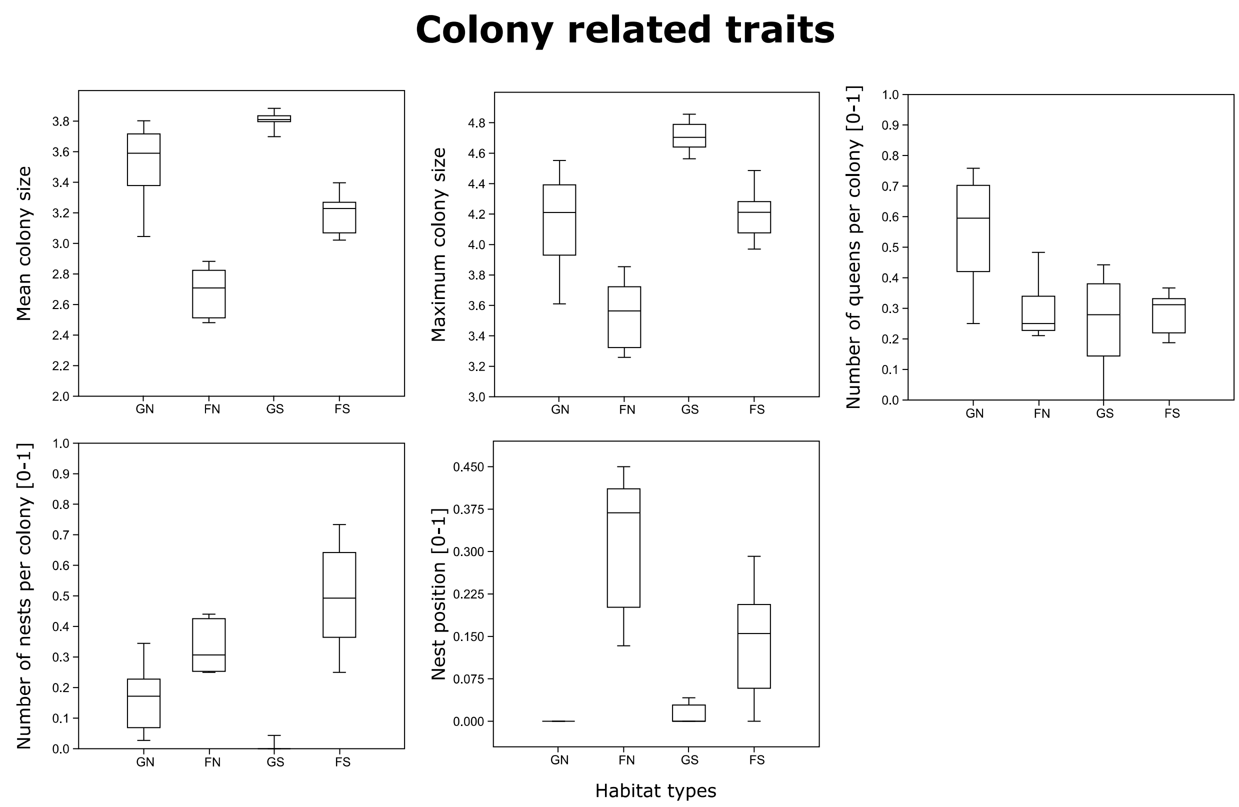

*Figure 11.* Box plots of the five colony related traits. Mean colony size and maximum colony size were measured log-transformed for a clearer visualization. An ordinal scale was used for the number of queens per colony (0: strictly monogynous, 0.5: facultatively polygynous, 1: usually polygynous) and number of nests per colony (0: monodomous, 0.5: facultatively polydomous, 1: usually polydomous). Nest position was measured on a binary scale (0: nest in/on ground layer, 1: nest at least sometimes arboreal, above ground layer).

Colony related traits (Fig. 11) showed to be heavily influenced by the exposition to flood risk. Ant species that thrive on sites with flood risk have on average significantly larger colonies than those on the northern sites, for both mean and maximum colony size. Ant species inhabiting the northern grassland showed a clear tendency towards polygyny, while the southern grassland species were predominantly monogynous. In the forest habitats no significant difference in queen numbers between northern and southern sites were observed.

With regard to numbers of nests and nest position, ant species showed a stronger difference between the habitats than in relation to flood risk. Ant species on grassland sites were predominantly monodomous, the species on the southern sites even almost exclusively so. While colonies of most ant species at the northern forest sites usually inhabit a single nest, the tendency towards living in polydomous colonies was significantly higher at the southern forest sites.

The position of the nest also varied more prominently with flooding risk in the forest than on meadows.

Nests of ant species occurring in the grassland are built on the ground level. In the forest, the nest position is surprisingly a lot and significantly higher in the non-flooded area than in the flood-prone area.

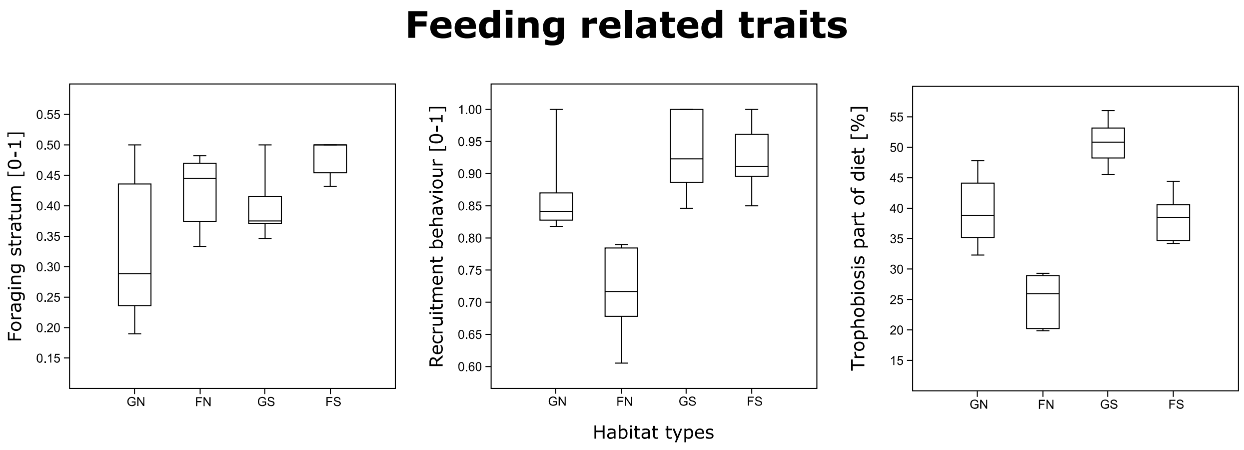

*Figure 12.* Box plots of the feeding related traits. An ordinal scale was used for foraging stratum (0: strictly on ground, 0.5: ground and arboreal, 1: arboreal foraging important) and recruitment behaviour (0: foraging individually, 0.5: group recruitment, 1: mass recruitment). The importance of trophobiosis as a part of diet was given in percentages.

Flooding risk had a significant influence on feeding related traits (Fig.12) in both habitats. Foraging stratum tended to be shifted shift towards a combination of ground and arboreal foraging with increasing flood risk. Mass recruitment was the most likely form of recruitment behaviour through all four habitats, but more distinctly so at the southern sites. The amount of trophobiosis as part of the diet was significantly higher among ants in the area with flood risk compared to species of the same habitat type from the northern sites.

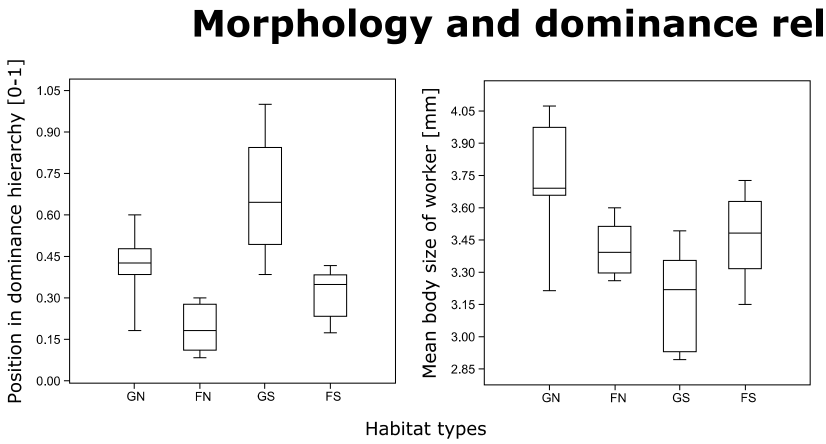

*Figure 13.* Box plots of morphology and dominance related traits. The position in the dominance hierarchy was scored on a binary scale (0: subdominant species, 1: dominant and territorial species). Mean body size of worker was expressed as length, measured from the tip of mandibles to tip of the gaster (mm).

Both position in dominance hierarchy and mean body size of worker were significantly related to flood risk. The shift towards more dominant ant species on the southern sites indicates a higher competitive pressure associated with the flood risk. Grassland ant species at sites with exposure to flood risk tended to be smaller on average. A similar effect did not exist between the forest habitat sites.

# Reproduction related traits

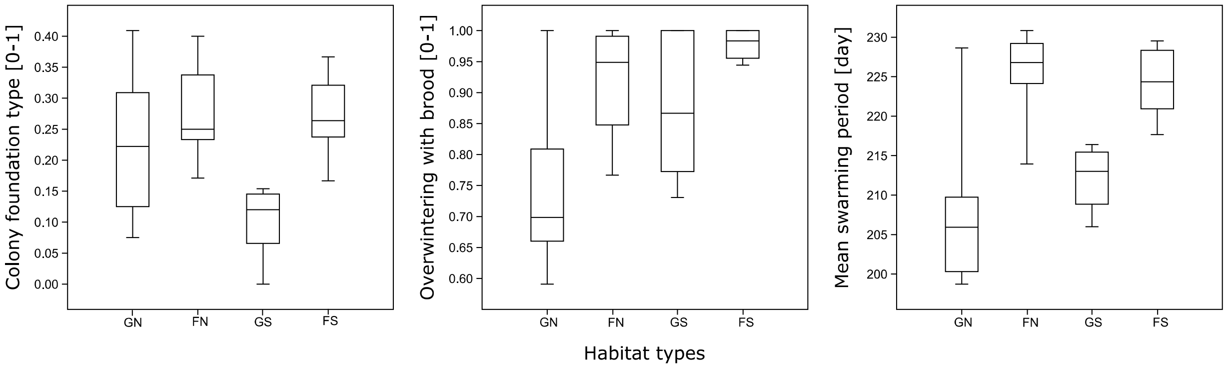

*Figure 14.* Box plots of reproduction related traits. Colony foundation type was expressed on an ordinal scale (0: independent colony foundation, 0.5: independent and dependent colony foundation, 1: dependent colony foundation). Overwintering with brood was measured on a binary scale (0: not overwintering with brood, 1: overwintering with brood). For the mean swarming period of winged sexuals the average calendar date was used as measurement unit.

Flood risk was clearly associated with higher values of reproduction related traits among grassland species. In the southern sites, ant species were significantly more likely to found a new colony independently than on northern sites, where a combination of independent and dependent colony foundation was more likely. In both forest habitats, establishing of a new colony is most likely to be achieved by a combination of dependent and independent foundation without a clear difference between northern and southern sites. Ant species that overwinter with brood were significantly more frequent in the southern sites than in the northern sites of the same habitat. The mean swarming date was not significantly influenced by flood risk.

*Table 5.* Results of two-way ANOVAs for the community weighted means of traits. For the traits which showed a significant interaction, Tukey's post-hoc test was performed to identify the significant differences between variables. *: significant at p < 0.05.

| Trait | Two-Way-ANOVA | | | | | | Tukey's Post-Hoc test for Interactions | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **mean colony size** | | Sum of Squares | Degrees of freedom | Mean square | F | p | | | Q | p |
| | Habitat: | 4.32 | 1 | 4.32 | 168.4 | <0.01* | grassland-no | grassland-yes | 4.74 | <0.01* |
| | Flood Risk: | 1.21 | 1 | 1.21 | 47.28 | <0.01* | grassland-no | forest-no | 15.11 | <0.01* |
| | Interaction: | 0.12 | 1 | 0.12 | 4.57 | 0.04* | grassland-yes | forest-yes | 10.84 | <0.01* |
| | Within: | 0.72 | 28 | 0.03 | | | forest-no | forest-yes | 9.01 | <0.01* |
| | Total: | 6.37 | 31 | | | | | | | |
| **maximum colony size** | | | | | | | | | | |
| | Habitat: | 2.5 | 1 | 2.5 | 58.35 | <0.01* | | | | |
| | Flood Risk: | 2.94 | 1 | 2.94 | 68.87 | <0.01* | | | | |
| | Interaction: | 0.02 | 1 | 0.02 | 0.43 | 0.52 | | | | |
| | Within: | 1.2 | 28 | 0.04 | | | | | | |
| | Total: | 6.66 | 31 | | | | | | | |
| **number of queens per colony** | | | | | | | | | | |
| | Habitat: | 0.12 | 1 | 0.12 | 7.47 | 0.01* | grassland-no | grassland-yes | 6.77 | <0.01* |
| | Flood Risk: | 0.17 | 1 | 0.19 | 11.71 | <0.01* | grassland-no | forest-no | 6.08 | <0.01* |
| | Interaction: | 0.18 | 1 | 0.18 | 11.23 | <0.01* | grassland-yes | forest-yes | 0.62 | 0.9 |
| | Within: | 0.45 | 28 | 0.02 | | | forest-no | forest-yes | 0.07 | 0.99 |
| | Total: | 0.93 | 31 | | | | | | | |
| **number of nests per colony** | | | | | | | | | | |
| | Habitat: | 0.87 | 1 | 0.87 | 76.54 | <0.01* | grassland-no | grassland-yes | 4.22 | 0.02* |
| | Flood Risk: | <0.01 | 1 | <0.01 | <0.01 | 0.96 | grassland-no | forest-no | 4.48 | 0.01* |
| | Interaction: | 0.21 | 1 | 0.21 | 18.27 | <0.01* | grassland-yes | forest-yes | 13.02 | <0.01* |
| | Within: | 0.32 | 28 | 0.01 | | | forest-no | forest-yes | 4.32 | <0.01* |
| | Total: | 1.39 | 31 | | | | | | | |
| **nest postiton** | | | | | | | | | | |
| | Habitat: | 0.4 | 1 | 0.4 | 68.11 | <0.01* | grassland-no | grassland-yes | 0.37 | 0.96 |
| | Flood Risk: | 0.05 | 1 | 0.05 | 9.26 | 0.01* | grassland-no | forest-no | 11.66 | <0.01* |
| | Interaction: | 0.07 | 1 | 0.07 | 11.64 | <0.01* | grassland-yes | forest-yes | 4.84 | 0.01* |
| | Within: | 0.17 | 28 | 0.01 | | | forest-no | forest-yes | 6.46 | <0.01* |
| | Total: | 0.69 | 31 | | | | | | | |
| **foraging stratum** | | | | | | | | | | |
| | Habitat: | 0.08 | 1 | 0.08 | 16.37 | <0.01* | | | | |
| | Flood Risk: | 0.04 | 1 | 0.04 | 7.59 | 0.01* | | | | |
| | Interaction: | <0.01 | 1 | <0.01 | 0.14 | 0.71 | | | | |
| | Within: | 0.13 | 28 | <0.01 | | | | | | |
| | Total: | 0.24 | 31 | | | | | | | |
| **recruitment behaviour** | | | | | | | | | | |
| | Habitat: | 0.05 | 1 | 0.05 | 13.7 | <0.01* | grassland-no | grassland-yes | 3.52 | 0,048* |
| | Flood Risk: | 0.15 | 1 | 0.15 | 44.33 | <0.01* | grassland-no | forest-no | 6.84 | <0.01* |
| | Interaction: | 0.03 | 1 | 0.03 | 9.86 | <0.01* | grassland-yes | forest-yes | 0.56 | 0.92 |
| | Within: | 0.1 | 28 | <0.01 | | | forest-no | forest-yes | 9.8 | <0.01* |
| | Total: | 0.33 | 31 | | | | | | | |
| **trophobiosis** | | | | | | | | | | |
| | Habitat: | 0.15 | 1 | 0.15 | 86.84 | <0.01* | | | | |
| | Flood Risk: | 0.12 | 1 | 0.12 | 70.88 | <0.01* | | | | |
| | Interaction: | <0.01 | 1 | <0.01 | 0.49 | 0.49 | | | | |
| | Within: | 0.05 | 28 | <0.01 | | | | | | |
| | Total: | 0.32 | 31 | | | | | | | |
| **position in dominance hierarchy** | | | | | | | | | | |
| | Habitat: | 0.66 | 1 | 0.66 | 35.78 | <0.01* | | | | |
| | Flood Risk: | 0.28 | 1 | 0.28 | 15.45 | <0.01* | | | | |
| | Interaction: | 0.03 | 1 | 0.03 | 1.37 | 0.25 | | | | |
| | Within: | 0.51 | 28 | 0.02 | | | | | | |
| | Total: | 1.48 | 31 | | | | | | | |
| **mean worker size** | | | | | | | | | | |
| | Habitat: | <0.01 | 1 | <0.01 | 0.02 | 0.9 | grassland-no | grassland-yes | 7.36 | <0.01* |
| | Flood Risk: | 0.45 | 1 | 0.45 | 10.39 | <0.01* | grassland-no | forest-no | 4.27 | 0.01* |
| | Interaction: | 0.74 | 1 | 0.74 | 17.12 | <0.01* | grassland-yes | forest-yes | 4.01 | 0.02* |
| | Within: | 1.21 | 28 | 0.04 | | | forest-no | forest-yes | 0.91 | 0.8 |
| | Total: | 2,4 | 31 | | | | | | | |
| **colony foundation type** | | | | | | | | | | |
| | Habitat: | 0.09 | 1 | 0.09 | 15.17 | <0.01* | grassland-no | grassland-yes | 4.73 | <0.01* |
| | Flood Risk: | 0.03 | 1 | 0.03 | 5.73 | 0.02* | grassland-no | forest-no | 1.56 | 0.52 |
| | Interaction: | 0.03 | 1 | 0.03 | 5.43 | 0.03* | grassland-yes | forest-yes | 6.23 | <0.01* |
| | Within: | 0.17 | 28 | 0.01 | | | forest-no | forest-yes | 0.06 | 0.99 |
| | Total: | 0.33 | 31 | | | | | | | |
| **overwintering with brood** | | | | | | | | | | |
| | Habitat: | 0.16 | 1 | 0.16 | 17.82 | <0.01* | | | | |
| | Flood Risk: | 0.08 | 1 | 0.08 | 8.44 | 0.01* | | | | |
| | Interaction: | 0.01 | 1 | 0.01 | 1.52 | 0.22 | | | | |
| | Within: | 0.26 | 28 | <0.01 | | | | | | |
| | Total: | 0.51 | 31 | | | | | | | |
| **mean swarming period** | | | | | | | | | | |
| | Habitat: | 1802.5 | 1 | 1802.5 | 48.78 | <0.01* | | | | |
| | Flood Risk: | 23.81 | 1 | 23.81 | 0.64 | 0.43 | | | | |
| | Interaction: | 79.13 | 1 | 79.13 | 2.14 | 0.15 | | | | |
| | Within: | 1034.74 | 28 | 36.95 | | | | | | |
| | Total: | 2940.18 | 31 | | | | | | | |

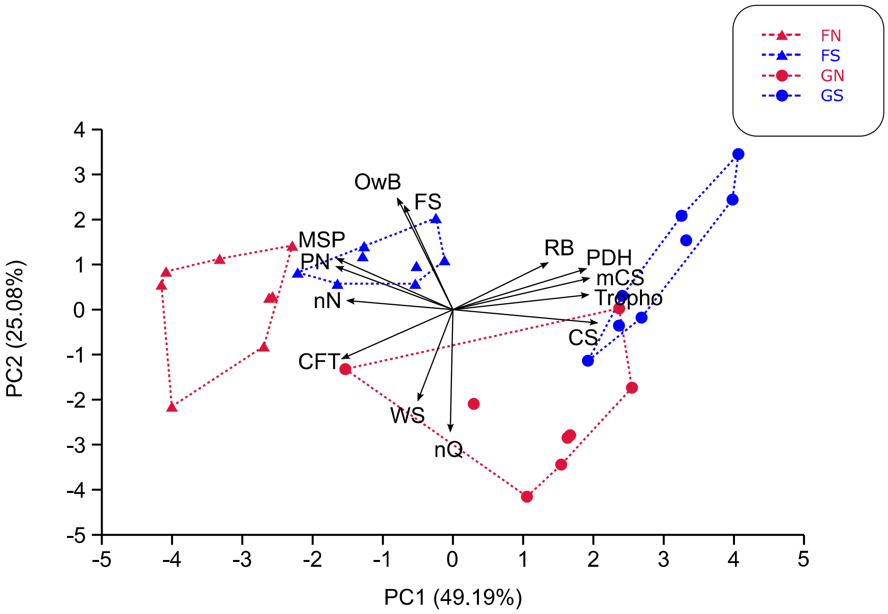

*Figure 15.* PCA of the ant community composition based on the community weighted means. The thirteen traits used for this ordination were mean worker size (WS), mean colony size (CS), maximum colony size (mCS), number of queens per colony (nQ), number of nests per colony (nN), colony foundation type (CFT), amount of trophobiosis in diet (Tropho), nest position (PN), foraging stratum (FS), overwintering with brood (OwB), mean swarming period (MSP), recruitment behaviour (RB) and position in dominance hierarchy (PDH). Values on the axis refer to the percentage of eigenvalues.

A principal component analysis performed based on the community weighted means reveals that certain traits show strong covariance, indicating that the expression of these traits play very similar roles for the establishment of ants in the environmental gradients under study (Fig. 15). Traits where the vectors are similar or nearly the same are overwintering with brood and foraging stratum in the southern forest sites, and position in dominance hierarchy and maximum colony size in the southern grassland sites. Besides the similarity of some trait vectors, the graphic shows for both forest and grassland habitats a clear separation into northern and southern sites. These differences were found to be significant with a two-way PERMANOVA (Tab. 6).

*Table 6.* Results of a two-way PERMANOVA showing that ant species composition displayed in the trait-based PCA ordination diagram is significantly affected by habitat type and flood risk. Permutation number was 9999, a Euclidean distance matrix was used for calculation. *: significant at p < 0.05.

| Source | Sum of squares | Degrees of freedom | Mean square | F | p |
|---|---|---|---|---|---|
| **Habitat** | 155.25 | 1 | 155.25 | 31.77 | <0.01* |
| **Flood Risk** | 76.89 | 1 | 76.89 | 15.74 | <0.01* |
| **Interaction** | 34.05 | 1 | 34.05 | 6.97 | <0.01* |
| **Residual** | 136.82 | 28 | 4.89 | | |
| **Total** | 403 | 31 | | | |

# 4. Discussion

## 4.1 Species richness and community composition

The 28 different ant species collected during this study represent nearly half of the 60 ant species known to occur in the national park area (Fellner et al., 2009; Schlick-Steiner & Steiner, 2002; Schlick-Steiner et al., 2005; Wagner et al., 2019; Wagner, 2019). All these 28 collected species were known to exist in the national park area.

The species accumulation curve showed a nearly complete coverage of the local ant fauna for the used sampling methods, leading to the conclusion that the rather high number of missed species is a result of mainly two factors: First, the choice of sampling methods which deliberately neglected socially parasitic species living as inquilines or strictly arboreal ant species. The second factor is the exclusion of a species-rich area, viz. the so-called Lobau, in the western part of the national park from this study, where due to river engineering and the resulting deepening of the Danube bed the dynamic floodplain character has been heavily influenced and partly been lost (Böttiger, 2011; Reckendorfer et al., 2012; Weigelhofer et al., 2013). The high amount of alluvial xeric habitats, the so-called "Heißländen", in this area contributes to a large part of the overall ant species richness of the Nationalpark Donau-Auen (Schlick-Steiner & Steiner, 2002; Steiner & Schlick-Steiner, 2004), but due to the changed dynamic floodplain character this area was not considered suitable as a study site for my own research questions. In addition to these two factors, some of the ant species known to occur in the national park area are rare and have only a low probability to be found, like the cryptic ant *Strumigenys argiola*, which has only been found in the national park area twice in 2008 (Fellner et al., 2009).

With eleven ant species exclusively found on meadow sites compared to eight species found exclusively on forest sites (Fig. 5), meadows account for a disproportionately large share of ant diversity, considering that most of the area of the national park is covered by forest. If the maintenance of these meadows were to be abandoned and the areas left to natural secondary succession in the direction of alluvial forest, this would result in a loss of a large part of the ant diversity.

The results of this study show a clear negative impact of flooding events on species richness of ants. This effect is much more pronounced in meadow than in forest habitats, with less than half the number of species (47%) found in flooded than in non-flooded meadow areas. The mean species richness of individual grassland sampling sites decreased from 6.5 in the non-flooded sites to 3 in the flooded sites, showing the huge constraining effect of the inundation on grassland-inhabiting ant species.

In forests, the effect of flooding on species richness was less evident with a total species number found in all flooded areas of 73% of the total species number of non-flooded areas. Only a slight decrease of the mean local species richness from 5.5 to 5 from non-flooded to flooded sites supports the conclusion that flooding events have a substantially more devastating effect on grassland-inhabiting ant species.

This outcome of different patterns depending on the habitat type is as expected, since the forests offer with the trees an escape possibility. Moreover, with the plethora of dead wood lying around structures are present, which provide at least short-term protection and shelter against flooding (Adis et al., 2001; Ballinger et al., 2007). In the meadows, on the other hand, there are no possibilities to retreat to a higher elevation level and no structures that offer at any kind of protection from flooding.

The few ant species which are able to survive on the flooded meadows are mostly generalists, which are known to inhabit disturbed dynamic habitats like *Formica cunicularia* (Seifert, 2018) and species which are known to be able to survive even week-long periods of inundation like *Lasius niger* and *Myrmica rubra* (Boomsma & Isaaks, 1982). Hence, near-annual flood events turned out to act as particularly powerful ecological filter for ants on meadows.

Species which are strongly associated with other ant species for reasons as colony foundation or temporary enslavement like *Lasius fuliginosus* or *Formica sanguinea* were only found in the non-flooded area. In case of *F. sanguinea* this is surprising, since this species is known to be highly adaptive for different habitat structures and is able to colonize new habitats in a short amount of time (Punttila et al., 1991; Seifert, 2018). With *Formica cunicularia* und *Formica rufibarbis* two *Serviformica* species were present at five of the eight sampled southern meadow sites, offering *F. sanguinea* a reasonable amount of possible slave workers. The complete absence of *L. fuliginosus* from flooded sites is less surprising since this species not only needs a long time to establish a new colony but is dependent on an established

*Chthonolasius* colony which can be invaded for colony foundation. And these *Chthonolasius* host species, in turn, are all again temporary social parasites of other *Lasius* species (Seifert, 2018) . Therefore, establishment of a temporary social hyperparasite like *L. fuliginosus* requires a particularly stable environment which apparently is not provided by near annually flood-prone forest stands.

An ant species that is known to occur in the national park area but was not sampled during this study is *Myrmica gallienii*. This species is especially remarkable for being the best adapted to flooding among the Central European ant species (Seifert, 2018). As this adaptation is accompanied by a strong hygrophily, a finding of this species on a southern sampling site would not have been surprising.

Noticeable is that with *Temnothorax crassispinus* only one *Temnothorax* species was collected during this study, while with *T. affinis, T.albipennis, T. clypeatus, T. corticalis, T. interruptus, T. parvulus* and *T. unifasciatus* at least seven other species of this genus are known to inhabit the national park area. However, the majority of these species are strongly or strictly arboricolous or occur only in xerothermic habitats (Seifert, 2018). Other, mostly xerothermophilous species inhabiting the national park area but not present in this study are several *Formica*-species as *F. truncorum, F. polyctena, F. pratensis, F. rufa, F. clara, F. fusca* and *F. fuscocinerea*. Especially the xerothermophilous species are most likely to be found in the western part of the national park, viz. the so-called Lobau, but the possibility cannot be excluded that some of these species also occur in the sampled dry meadows north of the dam and were not recorded during the sampling.

Ant community composition is shaped by both biotical and abiotical factors. While in this study I mostly focused on the abiotic factor of habitat disturbance by inundation, the biotic factor of interspecific competition cannot be ignored completely. Numerous studies have shown that especially in temperate climate zones ant community composition is strongly influenced by interspecific competition (Cerdá et al., 2013; Guariento & Fiedler, 2021; Hölldobler & Wilson, 1990; Peral et al., 2016). Since all ant species which occupy a high rank in the competitive hierarchies in their habitats (Seifert, 2017, 2018) were either just found on a single site each (in case of *L. fuliginosus* and *F. sanguinea*) or on all sites of the same habitat type (in case of *M. rubra* being found in all forest sites), it was not possible to make a reliable statement about their influence on the community composition of the other ant species.

Although flooding events had only little effect on species richness in forest habitats, the analysis of the community composition showed a more detailed picture. The nearly complete overlapping of the Pitfall clusters between flood-prone and flood-safe forest sites (Fig. 9) indicates that flooding risks are hardly relevant for these ant species. Contrary to this, the clusters of species collected with Winkler extraction showed no overlapping, corroborating a clear influence of the flooding risk on these species. This result comes as no surprise, since earlier studies showed that ant species collected by Winkler extraction in temperate zones are likely to be smaller, less active and more likely to build their nests on ground level than species collected by pitfall traps (Ivanov & Keiper, 2009; Martelli et al., 2004). These characteristics possibly render them more susceptible to inundation events.

The results of the analysis of community composition of the meadow sides support the results of the species richness, showing a clear effect for both Winkler and Pitfall sampled ant species and again underlining the devastating effect of near-annual flooding on ant species inhabiting grasslands.

The results of the CCA (Fig. 10) emphasized that the factor with the biggest influence on ant community composition was not the exposition to flooding risk per se, but the habitat type. This comes as no surprise since meadows and forests offer very different conditions, with habitat openness, the amount of available dead wood, different food sources, and the amount of leaf litter, just to name a few. With only 9 of the 28 collected species being found in both habitat types (Fig.5), this is the factor shaping ant community composition the most.

The results of both species richness and community composition are similar to the findings of Ballinger et al. (2007), Lude et al. (1999) and Mertl et al. (2009), who all showed a clear decrease of species richness and change of community composition with increasing flooding risk. New, but not surprising is the observation that the effect of recurring flooding events on ant fauna is clearly more distinct in grassland than in forest habitats.

To compare the impact of flooding events with other types of habitat disturbance, the distinction between transient habitat disturbance and lasting transformation is important. While habitat disturbance is defined as any event that removes biomass (Townsend & Hildrew, 1994), transformation means any changes in the availability of resources, the microclimate or structure of the habitat (Andersen, 2000; Philpott et al., 2010). Flooding events are both disturbing habitats and transforming them, since they remove biomass, yet also change the habitat by removing or re-arranging vegetation, soil and litter (Philpott et al., 2010). However, this kind of habitat transformation is usually less permanent and less severe than other, like fire, agriculture or pastoralism.

A lot of types of habitat disturbances have a greater impact on the ant fauna of closed canopy habitats like forests, since many habitat disturbances like fire, agriculture or pastoralism are usually transforming parts of closed forest habitats into open habitats (Andersen, 2019). Since ant communities usually differ between closed and open habitats, the effect of those disturbances is much more severe for those species inhabiting the habitat type which is transformed (Andersen, 2019; Vasconcelos et al., 2017). However, the flooding events occurring in the Nationalpark Donau-Auen are not severe enough to cause serious damage to the forests and transform them into an open habitat by destroying or removing a larger number of trees. Instead, this transformation is limited to major soil and litter disruption, explaining why the litter-dwelling species are particularly affected.

The observed loss in species richness and changed community composition of the ant species on the meadow sites seems even more remarkable since the last extreme flooding event in the Nationalpark Donau-Auen occurred in June 2013. All later flooding between 2014 and the data collection in 2020 were considerably weaker (Fig 1). This emphasizes how vulnerable most ant species are against this type of disturbance, if their habitat does not provide any kind of structure serving as protection or refugial area. Considering that not all meadows south of the dam are flooded every year, but especially when extreme floods occur, such as in 2013 and 2002, the results of my research suggest that these extreme events are leaving a legacy that can be traced in the ant community composition over many years.

While the aforementioned river regulation and deepening of the riverbed lead to changed flood dynamics that limit the frequency, duration and range of regular flood events, extreme floods are expected to increase due to climate change (Klasz et al., 2014; Kundzewicz et al., 2005; Marchi et al., 2010; Rajczak et al., 2013). The two rather recent extreme inundations of the Danube in 2002 and 2013, which in their extent would be more typical to occur once in a century, are consistent with the predictions that increased rainfall due to climate change, will increase the frequency of extreme summer floods in Central Europe (Kundzewicz et al., 2005).

On the long-term, these changed flood dynamics are likely to have a different influence on the ant community composition. During a long phase of very low floods over several subsequent years, various flood-sensitive ant species could establish south of the dam. It can be assumed that in the event of an extreme flood, almost all ant species on the southern side will become locally extinct. Overall, it can be assumed that the (re-)colonization-extinction cycle will extend over a longer period of time, thus enabling a larger number of ant species to establish themselves, but that the extreme floods will be so strong that only very few species will be able to establish themselves permanently.

For most other terrestrial arthropod groups which have been subject to recent studies in the Nationalpark Donau-Auen, the effect of flood-exposition on species richness differed from my findings. Only Fies et al. (2016) found a modest decline in species richness of butterflies on flooded meadows. Contrary to this, research on grasshopper assemblages by Demetz et al. (2013) revealed no difference in species richness between flooded and non-flooded meadows. Studies on moth communities in the riparian forests of the national park by Truxa and Fiedler (2012) and on wild bee communities on meadows by Neumüller et al. (2018) even suggest that for both groups the diversity is higher on flooded habitats. The drivers behind these observations are as diverse as the results of the individual studies, but they show that flood events are not generally beneficial or detrimental to terrestrial arthropod diversity.

These studies suggest that inundation events can represent a moderate disturbance for some terrestrial arthropod groups such as wild bees or moths, and, in accordance with the intermediate disturbance hypothesis, lead to higher species diversity than in undisturbed habitats (Connell, 1978; Lepori & Malmqvist, 2009). The effect of the same disturbance on ants however is too severe and leads to a significant decrease in diversity.

Within this series of arthropod studies carried out in the Nationalpark Donau-Auen, ants are the arthropod group that is the most sensitive to inundation events.

This investigated sensitivity could prove useful for further use of ants as bioindicators when monitoring transformations in the national park area. Ants are considered to be good indicators for a variety of environmental disturbances, especially those resulting from anthropogenic influences. In the Nationalpark Donau-Auen, a strong increase in species richness on a meadow located south of the dam could be a clear sign that this meadow has not experienced substantial flooding in the past years and might lose or has already lost some functions of its typical floodplain character. The same conclusion can be drawn if the establishment of an ant species which is known to be extremely sensitive to flood-exposition, like *Tapinoma subboreale* or *Myrmica sabuleti,* is observed on such a meadow site.

It is likely that the step decline in ant diversity on the flood-prone meadows might have a direct and negative influence on the ecological services provided by ants. These ecological services include pollination, seed dispersal, pest control, bioturbation, soil formation and nutrient cycling (Losey & Vaughan, 2006; Perović et al., 2018) and are linked to both identity and abundance of species (Elizalde et al., 2020). As this study does not refer to abundance, no statement can be made in this respect, but the loss of numerous species in the southern meadows makes it likely that the ecological services are not provided to the same extent as in the species-rich northern meadows.

## 4.2. The role of species traits in shaping community patterns

More interesting with regard to the mechanisms shaping ant assemblages than just describing the net effects of flooding on species richness and community composition are the roles played by various species traits. The analysis of these traits helps to understand which characters are enabling ants to deal with recurring habitat disturbances and which life history traits render it impossible for some species to survive in areas with high flooding risk. Since the overall effect of flooding on the ant fauna was clearly higher in grassland, this discussion sets the focus on the differences that occurred between the grassland habitats or where the effect in both grassland and forest was similar.

Most interesting for understanding why certain species can occur at the heavily disturbed, flood-exposed grassland sites are the traits that showed a high covariance and strong expression in the southern grassland sites, as shown in the PCA of the community weighted means of species traits (Fig. 15). These traits are an overall large colony size (mean and maximum), a high position in the local dominance hierarchy, a high significance of trophobiosis as part of the diet, the ability of workers to organize mass recruitment, and an independent mode of colony foundation.

In general, species found on the flood-exposed sites tended to have larger colony sizes than ant species on the non-exposed sites. These results are valid for both mean and maximum colony sizes. Based on current knowledge of the life-history of ants (Kaspari & O'Donnell, 2003; Linksvayer & Janssen, 2009), it could have been expected that sites with reoccurring disturbances would favor the occurrence of ant species with a smaller colony size since there is a known trade-off between colony size and generation time, especially for ants that are relying on independent colony foundation (Molet et al., 2008; Peeters & Molet, 2010). Larger colony sizes can be advantageous against predators or competitors but are unlikely to be more resistant against flooding per se. However, the shift towards larger colony sizes on the flooded sites is mostly driven by the exclusion or only rare sampling of some leaf-litter inhabiting species with an exceptionally small colony size on the flooded sites, such as *Ponera coarctata*, *Ponera testacea*, *Stenamma debile* and *Myrmecina graminicola* (Seifert, 2018*)*. Contrary to these species, *Solenopsis fugax* with a large colony size was present on both meadow habitats and not negatively influenced by the flooding risk. In conclusion, even if by the first impression it might appear that larger colony sizes are advantageous for ant species to survive in flood-exposed areas, this shift in the community weighted means is mostly driven by the exclusion of the named, weak in colony size, species. However, the reason for their exclusion might not be their small colony size but more likely that they are litter-dwelling and as such more harshly affected by the habitat disturbance and transformation.

For the species found in grassland habitats, a clear shift towards monodomy and monogyny in the flood-exposed areas could be observed. These traits go along with a shift from a mix of independent and dependent colony foundation towards rather strict independent colony foundation. Monodomy, monogyny and independent colony foundation are all traits that are commonly to be found in unstable habitats since they allow a rapid (re-)colonization following local extinctions after strong inundations. Independent colony founding is here especially advantageous, since this type of colony establishment usually goes along with a long-distance dispersal of mated gynes (Seifert, 2018).

Polydomy, polygyny and colony foundation by formation of daughter nests , in contrast, are traits usually found in habitats with stable conditions (Seifert, 2018). This is especially true for polygyny which is often connected to dependent colony foundation and comes with the disadvantage of a smaller dispersal range (Keller, 1995).

The observed shift of these traits can be interpreted as a sign that ant species found in the southern grassland sites are fast in recolonizing this habitat after a flooding event than being able to survive on site during flooding.

The same set of traits showed only little differences between the flooded and non-flooded forest areas, only a tendency towards more pronounced polydomy in the flooded areas was noticeable.

Polydomy can be a successful survival strategy in areas that are not completely affected by an occurring habitat disturbance, as a larger number of nests increases the chance that at least some nests will be spared from disturbance and remain available for the surviving colony (Debout et al., 2007). As it cannot be expected that any areas of the meadow sites may be spared from flooding, polydomy would not increase the survival chance of an ant colony since with high probability all nests will be destroyed by flooding. In the forest sites, however, since they offer some refugial areas as mentioned above, establishing several nests could be a key strategy for survival.

When it comes to the community weighted means of the traits of foraging stratum and the role of trophobiosis in the diet, again the loss of the litter-inhabiting species on the flooded sites is the main driver behind the shift between flooded and non-flooded-sites. Litter-dwelling species are foraging on the ground level, most of them exclusively (Theunis et al., 2005). Although there is a number of possible subterrean partners available for trophobiosis, interaction with trophobiotic partners does not contribute to a large amount of their diet for most of the litter inhabiting species sampled during this study (Seifert, 2018).

Using trophobiotic interactions as a major part of the diet may provide an advantage for species who are (re-)colonizing areas after habitat disturbance, given that the trophobiotic partner survived on site. For most non-arboreal trophobiotic partners it can be assumed that they are also heavily affected by flooding events and are rather fast in recolonizing after the flood instead of surviving on site. Aphids, which represent the most important group of trophobiotic partners in Central Europe, are known to have a short generation period and possess a combination of parthenogenetic and sexual reproduction. These traits are resulting in a rapid multiplication and together with winged individuals specialized for dispersal enable a quick recolonization after habitat disturbance (Stadler & Dixon, 2005; Stadler et al., 2003). Hence it can be expected that these aphids are recolonizing the disturbed sites directly after flooding events and are present on site already again when a new ant colony is establishing. Arboreal trophobiotic partners like *Cinara* or *Stomaphis* are unlikely to be affected by inundation events and are permanent and profitable partners for various *Formica* species respectively *L. fuliginousus (Schlaghamerský et al., 2013; Stadler & Dixon, 2008).* Seifert (2018) describes the Central European ant species as rather inclusive and opportunistic in their relations with the honeydew producing aphid species, with *Lasius flavus* being associated with at least 22 aphid species. Since Central European ant species are usually able to gain honeydew from a variety of aphid species, chances are good that they may find any suitable trophobiotic partner after (re-)colonization. Making use of this food resource may be an advantage over competitors who, if at all, only get a small proportion of their nutrition from trophobiosis.

The analysis of the community weighted means of species traits shows a shift towards a higher position in dominance hierarchy for the ant species found on the flood-exposed meadow sites, going along with a higher likelihood that the workers have the ability to organize mass recruitment. Dominance hierarchy in ant ecology is typically understood as a combination of aggressive interspecific encounters, resource monopolization and territoriality (Stuble et al., 2017). Due to this underlying combination of different traits, it is no surprise that the ability of mass recruitment and large colony sizes showed a high covariance with a high position in dominance hierarchy.

The analysis of species characteristics suggests that the few species that occur in the habitat most affected by the flood are mainly opportunists. Due to their type of colony foundation, the use of diverse food resources and a high tolerance of habitat conditions, it can be assumed that the ant fauna on the southern grassland sites is dominated by opportunistic species which can act as pioneer species after every catastrophic inundation event. An example of this is the presence of *Lasius niger* on all southern grassland sites, which is known to be a very potent pioneer species and survives well even in urban habitats (Seifert, 2017, 2018).

Trait-based analyses as the one used in this study are getting increasingly more popular in ecology, as the distribution of functional traits provides a better understanding of ecological processes than taxonomy alone (Perović et al., 2018). Since the use of trait-based analyses requires large datasets, trait-based global ecology was long dominated by plant ecologists with online databases such as LEDA and TRY (Bertelsmeier, 2017). There have been efforts to establish similar global trait databases for ants in the recent years such as Antprofiler (Bertelsmeier et al., 2013) and GlobalAnts (Parr et al., 2017). Only for few geographical regions an almost complete database for the most frequently studied traits exists. For the well-studied ant fauna of Central Europe, only the recent publications by Arnan et al. (2017) and Seifert (2017, 2018) have made available the information needed for a trait-based analysis. With the focus shifting to more trait-based ant ecology in the last decade, there have been several studies proving that this approach is a very promising method for a deeper understanding of ecological relationships (Arnan et al., 2018; Guilherme et al., 2019; Scharnhorst et al., 2021), especially regarding the concept of environmental filtering as in my research (Arnan et al., 2014; Boet et al., 2020). It is to be expected that with increasing knowledge about the traits of the individual species, the application of these trait-based approaches will continue to increase.

# 5. Conclusion

My working hypotheses on species richness and community composition were generally confirmed. Species richness was negatively affected by exposition to flooding and community composition was shaped by flooding risk. As expected, the effect of flood exposure on the ant communities was more severe on the grassland than forest sites. This was especially obvious in the impact on species richness, which was drastically reduced in flood exposed grasslands, whereas it was only marginally smaller in flood exposed forest sites compared to non-exposed forests. In the forests, the flooding impact on community composition was limited to ants inhabiting the leaf litter, while on grassland sites the whole community composition was affected by the inundation risk.

The analysis of species traits revealed that the few ant species found in the sites most affected by flooding are rather opportunistic species than habitat specialists. The dominance of traits usually found among pioneer species leads to the conclusion that these habitats are mostly getting recolonized by these ants after every flood, and that these ants are not particularly well-adapted to surviving on site during the inundation event.

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# Appendix

*Table S1.* List of the sampling sites with their geographical coordinates, elevation above sea-level, habitat description, position to dam and name of study area. Sites which are located north of the dam area flood-protected, sites south of the dam have a flood risk.

| Site | Area | Habitat | Position to Dam | Longitude | Latitude | Elevation (m a.s.l.) |
|---|---|---|---|---|---|---|
| **FN1** | Orth | Forest | North | 48°08'17.6"N | 16°40'17.6"E | 150 |
| **FN2** | Orth | Forest | North | 48°08'36.9"N | 16°41'15.1"E | 151 |
| **FN3** | Orth | Forest | North | 48°08'13.3"N | 16°41'10.1"E | 149 |
| **FN4** | Orth | Forest | North | 48°08'17.0"N | 16°42'07.3"E | 150 |
| **FN5** | Stopfenreuth | Forest | North | 48°08'43.0"N | 16°52'32.8"E | 148 |
| **FN6** | Stopfenreuth | Forest | North | 48°08'34.3"N | 16°52'08.8"E | 148 |
| **FN7** | Stopfenreuth | Forest | North | 48°08'19.5"N | 16°51'34.6"E | 149 |
| **FN8** | Stopfenreuth | Forest | North | 48°08'28.0"N | 16°51'13.5"E | 147 |
| **FS1** | Orth | Forest | South | 48°07'52.8"N | 16°40'39.1"E | 149 |
| **FS2** | Orth | Forest | South | 48°07'53.8"N | 16°41'35.8"E | 150 |
| **FS3** | Orth | Forest | South | 48°07'31.8"N | 16°41'49.2"E | 151 |
| **FS4** | Orth | Forest | South | 48°07'42.7"N | 16°41'54.3"E | 152 |
| **FS5** | Stopfenreuth | Forest | South | 48°08'33.5"N | 16°53'10.3"E | 146 |
| **FS6** | Stopfenreuth | Forest | South | 48°08'19.2"N | 16°52'55.1"E | 144 |
| **FS7** | Stopfenreuth | Forest | South | 48°08'22.5"N | 16°52'35.9"E | 148 |
| **FS8** | Stopfenreuth | Forest | South | 48°07'56.6"N | 16°52'01.5"E | 147 |
| **GN1** | Orth | Grassland | North | 48°08'16.6"N | 16°40'12.2"E | 148 |
| **GN2** | Orth | Grassland | North | 48°08'38.9"N | 16°41'09.4"E | 149 |
| **GN3** | Orth | Grassland | North | 48°08'16.7"N | 16°41'07.5"E | 148 |
| **GN4** | Orth | Grassland | North | 48°08'20.5"N | 16°41'21.5"E | 148 |
| **GN5** | Stopfenreuth | Grassland | North | 48°08'39.3"N | 16°52'32.4"E | 144 |
| **GN6** | Stopfenreuth | Grassland | North | 48°08'37.4"N | 16°52'06.1"E | 144 |
| **GN7** | Stopfenreuth | Grassland | North | 48°08'27.5"N | 16°51'01.7"E | 144 |
| **GN8** | Stopfenreuth | Grassland | North | 48°08'31.5"N | 16°51'22.5"E | 144 |
| **GS1** | Orth | Grassland | South | 48°07'52.4"N | 16°40'31.2"E | 149 |
| **GS2** | Orth | Grassland | South | 48°07'49.7"N | 16°40'44.8"E | 149 |
| **GS3** | Orth | Grassland | South | 48°07'53.7"N | 16°41'20.5"E | 149 |
| **GS4** | Orth | Grassland | South | 48°07'40.8"N | 16°41'55.3"E | 149 |
| **GS5** | Stopfenreuth | Grassland | South | 48°08'42.3"N | 16°53'18.6"E | 141 |
| **GS6** | Stopfenreuth | Grassland | South | 48°08'28.7"N | 16°52'40.9"E | 143 |
| **GS7** | Stopfenreuth | Grassland | South | 48°08'22.4"N | 16°52'12.3"E | 144 |
| **GS8** | Stopfenreuth | Grassland | South | 48°07'59.6"N | 16°51'45.9"E | 144 |

*Table S2*. Traits of ant species used in this study. Abbreviations: **WS** = mean worker size, measured from the tip of mandibles to tip of the gaster (mm), **CS** = mean colony size (measured in absolute numbers), **mCS** = maximum colony size (measured in absolute numbers), **nQ** = number of queens per colony ( 0: strictly monogynous, 0.5: facultatively polygynous, 1: usually polygynous), **nN** = number of nests per colony (0: monodomous, 0.5: facultatively polydomous, 1: usually polydomous), **CFT** = colony foundation type (0: independent colony foundation, 0.5: independent and dependent colony foundation, 1: dependent colony foundation), **Tropho** = percentage of trophobiosis based diet of food intake(given in fractions), **PN** = nest position (0: nest in/on ground layer, 1: nest at least sometimes arboreal, above ground layer), **FS** = foraging stratum (0: strictly on ground, 0.5: ground and arboreal, 1: arboreal foraging predominant), **OwB** = overwintering with brood (0: no, 1: yes), **MSP** = mean swarming period (day of the year [1-365]), **RB** = recruitment behaviour (0: foraging individually, 0.5: group recruitment, 1: mass recruitment), **PDH** = position in dominance hierarchy (0: subdominant species, 1: dominant and territorial species). For the few cases where single trait information was not available for a specific species, traits from a closely related species were used. These extrapolated traits are marked in the trait matrix with two stars (**), the original traits which were copied are marked with one star (*).

| Species | WS | CS | mCS | nQ | nN | CFT | Tropho | PN | FS | OwB | MSP | ToF | PDH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Camponotus fallax* | 6.9 | 300 | 1000 | 0 | 0 | 0 | 0.21 | 1 | 1 | 1 | 130 | 0.5 | 0 |
| *Dolichoderus quadripunctatus* | 3.5 | 300 | 1500 | 0 | 1 | 0.5 | 0.13 | 1 | 1 | 0 | 206 | 1 | 0 |
| *Formica cunicularia* | 5.3 | 1400 | 5000 | 0.5 | 0 | 0 | 0.32 | 0 | 0.5 | 0 | 185 | 0.5 | 0 |
| *Formica rufibarbis* | 6 | 2000 | 5000 | 0.5 | 0 | 0 | 0.31 | 0 | 0.5 | 0 | 189 | 0.5 | 0 |
| *Formica sanguniea* | 7.5 | 5000 | 20000 | 0.5 | 0.5 | 1 | 0.48 | 0 | 0.5 | 0 | 199 | 1 | 1 |
| *Lasius brunneus* | 2.9 | 5000 | 60000** | 0 | 0 | 0 | 0.6 | 1 | 1 | 1 | 168 | 1 | 0 |
| *Lasius emarginatus* | 3.2 | 5000 | 60000** | 0 | 0 | 0 | 0.44 | 0 | 0.5 | 1** | 175 | 1 | 1 |
| *Lasius flavus* | 2.9 | 5000 | 100000 | 0.5 | 0.5 | 0 | 0.8 | 0 | 0 | 1 | 231 | 1 | 0 |
| *Lasius fuliginosus* | 4 | 30000 | 2000000 | 0 | 0 | 1 | 0.64 | 1 | 0.5 | 1 | 158 | 1 | 1 |
| *Lasius niger* | 3 | 5000 | 60000* | 0 | 0 | 0 | 0.56 | 0 | 0.5 | 1* | 206 | 1 | 1 |
| *Lasius paralienus* | 4.5 | 5000 | 20000 | 0 | 0 | 0 | 0.36 | 0 | 0.5 | 1** | 247 | 1 | 1 |
| *Lasius platythorax* | 3 | 5000 | 60000 | 0 | 0 | 0 | 0.56 | 0 | 0.5 | 1** | 207 | 1 | 1 |
| *Leptothorax gredleri* | 3.2 | 33 | 100 | 0 | 0 | 0.5 | 0.07 | 1 | 0.5 | 1 | 223 | 0.5 | 0 |
| *Myrmecina graminicola* | 3.05 | 45 | 136 | 0.5 | 0 | 0.5 | 0 | 0 | 0 | 1 | 238 | 0 | 0 |
| *Myrmica rubra* | 4 | 1600 | 20000 | 0.5 | 1 | 0.5 | 0.37 | 0 | 0.5 | 1 | 236 | 1 | 0 |
| *Myrmica ruginodis* | 4.75 | 800 | 6000 | 0.5 | 0.5 | 0.5 | 0.3 | 0 | 0.5 | 1 | 221 | 1 | 0 |
| *Myrmica sabuleti* | 4.4 | 650 | 1200 | 1 | 0 | 0.5 | 0.37 | 0 | 0.5 | 1 | 233 | 1 | 0 |
| *Myrmica schencki* | 4.15 | 350 | 930 | 0.5 | 0 | 0.5 | 0.27 | 0 | 0 | 1 | 234 | 1 | 0 |
| *Ponera coarctata* | 2.95 | 50 | 135* | 1 | 0 | 0.5 | 0 | 0 | 0 | 0* | 241 | 0.5 | 0 |
| *Ponera testacea* | 2.75 | 50 | 135** | 1 | 0 | 0.5 | 0 | 0 | 0 | 0** | 256 | 0.5 | 0 |
| *Solenopsis fugax* | 2.25 | 50000 | 200000 | 1 | 0 | 0.5 | 0.5 | 0 | 0 | 1 | 251 | 1 | 0 |
| *Stenamma debile* | 3.6 | 56 | 180 | 0.5 | 0 | 0.5 | 0.02 | 0 | 0 | 1 | 265 | 0 | 0 |
| *Tapinoma erraticum* | 2.8 | 2000 | 10000 | 1 | 1 | 0.5 | 0.2 | 0 | 0 | 1 | 172 | 1 | 1 |
| *Tapinoma subboreale* | 2.8 | 1500 | 2000 | 1 | 1 | 0.5 | 0.2 | 0 | 0 | 1 | 173 | 1 | 1 |
| *Temnothorax crassispinus* | 2.9 | 80 | 366 | 0 | 0 | 0 | 0.03 | 1 | 0.5 | 1 | 226 | 0.5 | 0 |
| *Tetramorium caespitum* | 2.9* | 15000* | 75000* | 0* | 0* | 0* | 0.35* | 0 | 0 | 1 | 178 | 1 | 1 |
| *Tetramorium immigrans* | 2.9** | 15000** | 75000** | 0** | 0** | 0** | 0.35** | 0 | 0 | 1 | 178 | 1 | 1 |
| *Tetramorium staerckei* | 2.9** | 15000** | 75000** | 0** | 0** | 0** | 0.35** | 0 | 0 | 1 | 164 | 1 | 1 |

*Table S3.* List of community weighted means of traits (CWM). The abbreviations for the traits are as named in Table S2. To create the community weighted means matrix, the values of the single traits were weighted according to the pseudo-abundances at the sampling site and then divided by the total number of incidences at this site.

| Site | WS | CS | mCS | nQ | nN | CFT | Tropho | PN | FS | OwB | MSP | ToF | PDH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **FN1** | 3.6 | 2.88209 | 3.85396 | 0.225 | 0.25 | 0.35 | 0.292 | 0.45 | 0.45 | 0.95 | 213.95 | 0.725 | 0.3 |
| **FN2** | 3.26579 | 2.48142 | 3.28631 | 0.23684 | 0.26316 | 0.23684 | 0.19868 | 0.36842 | 0.39474 | 1 | 229.57895 | 0.60526 | 0.15789 |
| **FN3** | 3.54833 | 2.49275 | 3.25901 | 0.48333 | 0.35 | 0.4 | 0.202 | 0.13333 | 0.33333 | 0.76667 | 230.83333 | 0.68333 | 0.1 |
| **FN4** | 3.39583 | 2.57402 | 3.43619 | 0.25 | 0.41667 | 0.25 | 0.20375 | 0.41667 | 0.45833 | 1 | 226.91667 | 0.70833 | 0.08333 |
| **FN5** | 3.38971 | 2.70607 | 3.51769 | 0.35294 | 0.25 | 0.25 | 0.26838 | 0.20588 | 0.36765 | 0.82353 | 224.23529 | 0.67647 | 0.20588 |
| **FN6** | 3.408 | 2.83932 | 3.74561 | 0.3 | 0.44 | 0.3 | 0.2932 | 0.2 | 0.44 | 0.92 | 226.68 | 0.78 | 0.24 |
| **FN7** | 3.3875 | 2.70994 | 3.60906 | 0.25 | 0.42857 | 0.23214 | 0.25054 | 0.39286 | 0.48214 | 0.96429 | 228.10714 | 0.78571 | 0.14286 |
| **FN8** | 3.26053 | 2.77853 | 3.65259 | 0.21053 | 0.26316 | 0.17105 | 0.28053 | 0.36842 | 0.47368 | 0.94737 | 224.10526 | 0.78947 | 0.28947 |
| **FS1** | 3.63478 | 3.06391 | 4.08183 | 0.32609 | 0.65217 | 0.32609 | 0.34391 | 0.17391 | 0.5 | 1 | 229.21739 | 0.91304 | 0.17391 |
| **FS2** | 3.72667 | 3.21635 | 4.28062 | 0.36667 | 0.73333 | 0.36667 | 0.38533 | 0.06667 | 0.5 | 1 | 229.53333 | 0.96667 | 0.2 |
| **FS3** | 3.61111 | 3.39656 | 4.48658 | 0.30556 | 0.61111 | 0.30556 | 0.44389 | 0 | 0.5 | 1 | 224.72222 | 1 | 0.38889 |
| **FS4** | 3.46667 | 3.082 | 4.0746 | 0.22917 | 0.45833 | 0.25 | 0.35417 | 0.20833 | 0.5 | 1 | 221.45833 | 0.89583 | 0.33333 |
| **FS5** | 3.42667 | 3.02103 | 3.96953 | 0.21667 | 0.36667 | 0.23333 | 0.342 | 0.2 | 0.48333 | 0.96667 | 220.76667 | 0.85 | 0.36667 |
| **FS6** | 3.15 | 3.25416 | 4.19418 | 0.1875 | 0.25 | 0.16667 | 0.38375 | 0.29167 | 0.5 | 0.95833 | 217.66667 | 0.89583 | 0.41667 |
| **FS7** | 3.49722 | 3.24066 | 4.28178 | 0.33333 | 0.52778 | 0.27778 | 0.41139 | 0.05556 | 0.44444 | 0.94444 | 224 | 0.94444 | 0.33333 |
| **FS8** | 3.27955 | 3.27413 | 4.22983 | 0.31818 | 0.36364 | 0.25 | 0.38795 | 0.13636 | 0.43182 | 0.95455 | 225.68182 | 0.90909 | 0.36364 |
| **GN1** | 3.6575 | 3.54171 | 4.4257 | 0.25 | 0.05 | 0.075 | 0.478 | 0 | 0.475 | 0.75 | 205.85 | 0.875 | 0.6 |
| **GN2** | 3.21429 | 3.32469 | 3.90318 | 0.62857 | 0.24286 | 0.31429 | 0.34243 | 0 | 0.22857 | 0.82857 | 210.91429 | 0.82857 | 0.48571 |
| **GN3** | 3.68793 | 3.60723 | 4.00977 | 0.75862 | 0.34483 | 0.2931 | 0.3231 | 0 | 0.18966 | 0.65517 | 199.24138 | 0.82759 | 0.41379 |
| **GN4** | 4.07273 | 3.04514 | 3.61024 | 0.72727 | 0.18182 | 0.40909 | 0.40455 | 0 | 0.5 | 1 | 228.63636 | 1 | 0.18182 |
| **GN5** | 3.69375 | 3.7244 | 4.28989 | 0.59375 | 0.125 | 0.21875 | 0.39188 | 0 | 0.26563 | 0.6875 | 206.25 | 0.84375 | 0.375 |
| **GN6** | 3.71757 | 3.80264 | 4.55216 | 0.37838 | 0.02703 | 0.09459 | 0.45351 | 0 | 0.31081 | 0.67568 | 206.02703 | 0.83784 | 0.43243 |
| **GN7** | 3.65968 | 3.69393 | 4.24443 | 0.59677 | 0.16129 | 0.22581 | 0.38452 | 0 | 0.25806 | 0.70968 | 203.51613 | 0.85484 | 0.41935 |
| **GN8** | 4.05909 | 3.57301 | 4.17738 | 0.54545 | 0.18182 | 0.21591 | 0.37932 | 0 | 0.31818 | 0.59091 | 198.72727 | 0.81818 | 0.45455 |
| **GS1** | 3.1875 | 3.80918 | 4.74866 | 0.2 | 0 | 0.075 | 0.526 | 0 | 0.425 | 0.9 | 211.05 | 0.95 | 0.75 |
| **GS2** | 2.9075 | 3.84122 | 4.79224 | 0.225 | 0 | 0.125 | 0.5335 | 0 | 0.375 | 1 | 216.4 | 1 | 0.75 |
| **GS3** | 3 | 3.69897 | 4.77815 | 0 | 0 | 0 | 0.56 | 0 | 0.5 | 1 | 206 | 1 | 1 |
| **GS4** | 2.89375 | 3.88361 | 4.85562 | 0.125 | 0 | 0.0625 | 0.52625 | 0 | 0.375 | 1 | 208.125 | 1 | 0.875 |
| **GS5** | 3.25 | 3.79491 | 4.63673 | 0.33333 | 0 | 0.125 | 0.48208 | 0.04167 | 0.375 | 0.83333 | 214.91667 | 0.89583 | 0.54167 |
| **GS6** | 3.49231 | 3.81258 | 4.56331 | 0.44231 | 0 | 0.15385 | 0.455 | 0.03846 | 0.34615 | 0.73077 | 215.61538 | 0.84615 | 0.38462 |
| **GS7** | 3.34783 | 3.81814 | 4.65921 | 0.3913 | 0.04348 | 0.15217 | 0.48391 | 0 | 0.36957 | 0.78261 | 214.47826 | 0.8913 | 0.47826 |
| **GS8** | 3.35769 | 3.80216 | 4.64977 | 0.34615 | 0 | 0.11538 | 0.49077 | 0 | 0.38462 | 0.76923 | 211.53846 | 0.88462 | 0.53846 |

*Table S4.* Vegetation data of the single sites. Flood Risk was coded as no (0) or yes (1). Litter density was measured in cm, litter coverage, grass coverage and canopy density are listed as percentages.

| Site | Flood Risk | Litter Density | Litter Coverage | Grass Coverage | Canopy Density |
|---|---|---|---|---|---|
| **FN1** | 0 | 2.46666 | 80 | 0 | 94.83129 |
| **FN2** | 0 | 1.61666 | 66.66666 | 0 | 91.70109 |
| **FN3** | 0 | 1.05 | 63.33333 | 0 | 95.06745 |
| **FN4** | 0 | 2.91666 | 86.66666 | 0 | 94.94423 |
| **FN5** | 0 | 3.08333 | 60 | 0 | 93.09851 |
| **FN6** | 0 | 1.85 | 60 | 0 | 89.82345 |
| **FN7** | 0 | 2.53333 | 88.33333 | 0 | 86.01615 |
| **FN8** | 0 | 1.68333 | 60 | 0 | 94.98721 |
| **GN1** | 0 | 0,8 | 51.66666 | 100 | 0 |
| **GN2** | 0 | 2.58333 | 73.33333 | 95 | 0 |
| **GN3** | 0 | 0.71666 | 41.66666 | 80 | 0 |
| **GN4** | 0 | 1.35 | 95 | 90 | 0 |
| **GN5** | 0 | 0.43333 | 58.33333 | 85 | 0 |
| **GN6** | 0 | 0.55 | 65 | 100 | 0 |
| **GN7** | 0 | 0.48333 | 90 | 90 | 0 |
| **GN8** | 0 | 0.56666 | 65 | 80 | 0 |
| **FS1** | 1 | 2.65 | 66.66666 | 0 | 94.08196 |
| **FS2** | 1 | 1.76666 | 76.66666 | 0 | 95.15161 |
| **FS3** | 1 | 2.36666 | 76.66666 | 0 | 95.59411 |
| **FS4** | 1 | 1.15 | 50 | 0 | 92.24713 |
| **FS5** | 1 | 2.31666 | 70 | 0 | 95.21419 |
| **FS6** | 1 | 1.36666 | 70 | 0 | 72.03819 |
| **FS7** | 1 | 2.08333 | 68.33333 | 0 | 92.73074 |
| **FS8** | 1 | 2.48333 | 53.33333 | 0 | 94.14956 |
| **GS1** | 1 | 1.05 | 90 | 90 | 0 |
| **GS2** | 1 | 0.91666 | 88.33333 | 100 | 0 |
| **GS3** | 1 | 1.4 | 96.66666 | 100 | 0 |
| **GS4** | 1 | 1.21666 | 0.83333 | 100 | 0 |
| **GS5** | 1 | 0.78333 | 70 | 80 | 0 |
| **GS6** | 1 | 0.71666 | 71.66666 | 90 | 0 |
| **GS7** | 1 | 0.66666 | 78.33333 | 100 | 0 |
| **GS8** | 1 | 0.81666 | 73.33333 | 100 | 0 |

# Abstract

Several recent studies have focused on the influence of reoccurring flooding events on the Central European invertebrate fauna, proving that flooding influences species richness and/or community composition. Ants as terrestrial and mostly stationary invertebrates with a long colonial lifecycle are expected to be more vulnerable to the habitat disturbance caused by flooding than other invertebrates studied so far.

This study investigates differences in ant species richness and community composition between flood-protected and flood-prone meadow and forest sites in a Central European floodplain region. 28 different ant species were collected with pitfall traps and Winkler extraction. 13 species-specific life-history traits of ants were analyzed to understand the drivers behind the observed species distribution.

Flood-exposition affected species richness and community composition differently depending on the habitat studied.

On the meadow sites, increased flooding risk led to a strong decrease in species richness and an overall change in community composition. On forest sites, increased flooding risk had less influence on species richness and only changed the composition of the litter-inhabiting ant community.

The trait analysis showed a clear shift towards monogyny, monodomy, independent colony establishment and a high position in the local dominance hierarchy for the few ant species found on the flood exposed meadow sites.

Based on the negative connection between flood-exposition and species richness, ants are a suitable indicator for changes in the floodplain region. A significant increase in species richness or occurrence of especially flood-sensitive ant species can indicate that a site is losing its typical floodplain-character.

*Key words: Formicidae, species richness, community composition, flood-exposition, inundation, functional traits, Nationalpark Donau-Auen*

## Zusammenfassung

Mehrere aktuelle Studien haben sich mit dem Einfluss wiederkehrender Überschwemmungen auf die mitteleuropäische Wirbellosenfauna befasst und nachgewiesen, dass Überschwemmungen den Artenreichtum und/oder die Zusammensetzung der Artgemeinschaften beeinflussen. Es ist zu erwarten, dass Ameisen als terrestrische und meist stationäre Invertebraten mit einem langen kolonialen Lebenszyklus anfälliger für die durch Überschwemmungen verursachte Störung ihres Lebensraums sind als andere bisher untersuchte Invertebraten.

In dieser Studie werden die Unterschiede im Artenreichtum und in der Zusammensetzung der Ameisengemeinschaften zwischen hochwassergeschützten und hochwassergefährdeten Wiesen- und Waldstandorten in einer mitteleuropäischen Auenregion untersucht. 28 verschiedene Ameisenarten wurden mittels Bodenfallen und Winkler-Extraktion gesammelt. 13 artspezifische *life-history*-Eigenschaften der Ameisen wurden analysiert, um die Ursachen für die beobachtete Artenverteilung zu verstehen.

Die Hochwasserexposition wirkte sich je nach untersuchtem Lebensraum unterschiedlich auf den Artenreichtum und die Zusammensetzung der Artgemeinschaft aus.

Auf den Wiesenstandorten führte ein erhöhtes Überschwemmungsrisiko zu einem starken Rückgang des Artenreichtums und zu einer allgemeinen Veränderung der Zusammensetzung der Artgemeinschaft. Auf Waldstandorten hatte ein erhöhtes Überschwemmungsrisiko nur geringen Einfluss auf den Artenreichtum und veränderte nur die Zusammensetzung der Ameisengemeinschaft, die Streu bewohnt.

Die Merkmalsanalyse zeigte bei den wenigen Ameisenarten, die auf den überschwemmungsexponierten Wiesenstandorten gefunden wurden, eine klare Verschiebung in Richtung Monogynie, Monodomie, unabhängige Koloniegründung und eine hohe Position in der lokalen Dominanzhierarchie.

Aufgrund des negativen Zusammenhangs zwischen Überschwemmungsexposition und Artenreichtum sind Ameisen ein aussagekräftiger Indikator für Veränderungen in der Auenregion. Ein deutlicher Anstieg des Artenreichtums oder das Vorkommen besonders hochwasserempfindlicher Ameisenarten kann darauf hinweisen, dass ein Standort seinen typischen Auencharakter verliert.