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Alluvial forest vegetation in an active and inactive alpine floodplain – a case study from River Ammer (Bavaria)

Auwaldvegetation im aktiven und inaktiven Bereich einer alpinen Wildflussaue am Beispiel der Ammer

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Abstract

Most alpine floodplains are heavily modified and have lost their natural habitat dynamics and biodiversity. However, little is known about the consequences for floodplain forests. To study this topic, the Bavarian River Ammer was selected. An analysis of the effects of river regulation was possible within the 'Schnalzaue' where 55 years ago a weir and a dam had been built separating an active and inactive section of the floodplain. A comparison between both sections helps assessing the effect of the dam on the alluvial grey-alder forests (*Alnetum incanae*), as basis for future restoration. We expected lower disturbance, lower moisture and higher nutrient supply in the inactive floodplain and thus, a transition to a maple-ash forest (*Adoxo-Aceretum*). Therefore, we analysed species composition, functional plant traits of the leaf-height-seed scheme (leaf dry matter content, plant height, seed mass) and Ellenberg indicators (indicator values for moisture and nutrients, indicator species for flooding and for periodical wet conditions). The ordination results indicated different species compositions in both floodplain sections, while this was poorly reflected by the results of a syntaxonomic analysis. The latter suggested presence of a rarely flooded *Asarum*-subassociation of grey-alder forest in both floodplain sections. In the sections, similar site conditions prevailed regarding moisture and nutrient supply, while plant height indicated slightly more disturbance in the active floodplain. Overall, the results reveal low disturbance in both sections, even though the active one is connected with the river. A reason for this finding could be increased erosion of River Ammer downstream the weir with respective lower water levels. Accordingly, restoration should improve river dynamics in the entire floodplain to allow more frequent disturbance as a measure to maintain the grey-alder forest in the long term.

Keywords: active floodplain, alluvial forest, *Alnetum incanae*, Ammer, dam, floodplain vegetation, functional plant trait, LHS scheme, weir

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

1.1 Threatened alluvial forests

Rivers and their floodplains are characterised by strong hydromorphological dynamics, making them some of the most productive and diverse ecosystems worldwide (JUNK et al. 1989, TOCKNER & STANFORD 2002). Unfortunately, technical constructions have altered the discharge and flooding regime of many catchments (TOCKNER & STANFORD 2002), with negative effects on floodplain vegetation. For example, weirs and dams cause a reduced disturbance regime which leads to changes in species composition and vegetation structure (LEYER 2004). Thus, alluvial forest vegetation is endangered due to human activities (OLSON & DINERSTEIN 1998, BERNHARDT et al. 2005, ELLWANGER et al. 2012). For example, Riparian alluvial forests of alder and ash are listed as 'near threatened (acute)' (category 3–V) in Germany (FINCK et al. 2017), because there is widespread succession of the remaining stands which are negatively affected by dams (BfN 2018: *Alnetum incanae* Lüdi 1921). However, few studies have investigated separated and therefore unflooded alluvial forests, and if they did, they mainly focussed on the shrub and tree layer (DEILLER et al. 2001, GERGEL et al. 2002). Thus, there is a need for investigations like GLAESER & WULF (2009) who specifically studied effects on the more sensitive herbaceous layer. In our study, we focussed on an alluvial forest combining a phytosociological approach with a trait-based analysis, because this combination of methods should produce a clearer picture of the ecosystem state and thus helps understanding ecosystem processes.

1.2 Floodplain forest communities

There are a number of forest associations described for alpine floodplains: for example, the *Alnetum incanae* for active floodplains (DOUDA et al. 2016) and the maple-ash forests (*Adoxo-Aceretum* Passarge 1960 nom. conserv. propos.) for inactive floodplain sections (PFADENHAUER 1969). The *Alnetum incanae* belongs to montane softwood forests and is situated between the mean summer high-water line and the mean annual high water (LEUSCHNER & ELLENBERG 2017), i.e., located between willow scrub (*Salicetum eleagno-purpureae* Sillinger 1933 nom. mutat. propos.) and maple-ash forest (*Adoxo-Aceretum*; SCHWABE 1985). This type of alluvial forest is characterised by periodic or episodic floods and marked groundwater fluctuations (SCHWABE 1985). In case of reduced flood frequency, the subassociation *Alnetum incanae asaretosum* with *Asarum europaeum* is present, and in case of drier habitats, the subassociation *Alnetum incanae caricetosum* with *Carex alba* occurs (SCHWABE 1985). *Adoxo-Aceretum* replaces the hardwood forest (*Querco-Ulmetum* Issler 1924) in mountainous areas (above 550 m a.s.l); it is related to the *Tilio platyphylli-Acerion pseudoplatani* Klika 1995 and represents the transition zone to alluvial forests (*Alno-Ulmion minoris* Br.-Bl. et Tx. ex Tchou 1948/1949 nom. conserve. propos.) (MÜLLER 1992). The *Adoxo-Aceretum* is found on colluvial or unflooded alluvial soils which are moist due to waterlogging, high groundwater levels or high precipitation (PFADENHAUER 1969). Finally, both associations are located on nutrient-rich and fresh to moist soils with a flowing and fluctuating groundwater (PFADENHAUER 1969, SCHWABE 1985). Although the herbaceous layer is very similar in both cases, the tree or shrub layers differ since annual floods only occur in the *Alnetum incanae*. For this reason, resulting from a lack of flood disturbance, the *Alnetum incanae* develops to a *Adoxo-Aceretum* (PFADENHAUER 1969).

1.3 Trait-based analysis of floodplain forests

The analysis of changes and differences in floodplain communities can benefit from using functional plant traits. Accordingly, we applied this approach to indicate relevant ecosystem processes and to achieve a comparison of the ecosystem conditions before and after floodplain restoration. The plant strategy 'leaf-height-seed scheme' (LHS) by WESTOBY (1998) provides a good orientation for a reliable selection of the most important functional plant traits (WEIHER et al. 1999, LAUGHLIN et al. 2010). The LHS scheme has been applied to various situations, such as plant communities from contrasting habitats (LAVERGNE et al. 2003), management strategies (MOOG et al. 2005), and grazing conditions (GOLODETS et al. 2009). The main innovation of LHS compared to the CSR scheme (GRIME 1974) is that it differentiates disturbance into spatio-temporal aspects. Furthermore, the LHS scheme forms a three-dimensional space with quantifiable values. It uses 'plant height at maturity' as indicator for growth rates between two disturbance events and 'seed mass' for considering the ability to establish in distant habitats (WESTOBY 1998, WESTOBY & WRIGHT 2006). WESTOBY (1998) describes the investment into height as a race for light which is restarted by every new disturbance event. For this reason, the trade-off ranges between a tall final height and high growth rates in early life stages (WESTOBY & WRIGHT 2006). Seed mass describes the trade-off between seed size and seed output (WESTOBY et al. 2002), since smaller seeds allow a production of more units per plant (HENERY & WESTOBY 2001) which may spread farther (WESTOBY 1998). Contrary, seedlings from bigger seeds are more successful in establishing under stressful conditions (LEISHMAN et al. 2000). Taking both traits into account, seed mass gives information about the spatial aspect of disturbance and the demographic aspect of a population at the stages of germination and establishment. Lastly, there is a need for a leaf trait which represents the local nutrient gradient (WESTOBY 1998, WRIGHT et al. 2004). Therefore, the 'leaf dry matter content' (LDMC) is a useful variable which is defined as leaf dry mass divided by fresh mass (HODGSON et al. 2011, PÉREZ-HARGUINDEGUY et al. 2013). The main advantage of LDMC is that it is unaffected by shade which is not the case for specific leaf area (HODGSON et al. 2011). Complementing the functional plant traits with Ellenberg indicator values offers detailed information about the dominant factors for plant communities.

1.4 Monitoring alluvial forests

Community descriptions and trait-based analyses can be used to monitor restoration of floodplain forests, as done in this study for the alpine River Ammer in southern Germany. In 1963, a longitudinal dam was built at 'Schnalzaue' in the middle reach of this river as part of a weir construction. Thus, the floodplain became divided into an inactive section above the weir behind the dam and an active section below the weir without a dam. Currently, a restoration project is planned to re-dynamize this river section including its floodplain by removing the dam and the weir (DIEHL et al. 2016).

The aim of this study was to check the long-term development of alluvial vegetation comparing the floodplain section that had been inactive for 55 years with the active one. We wanted to know how the dam had affected the herb layer of the alluvial forests. Thus, these observations provide a benchmark to investigate future success of the planned restoration. The following questions and hypotheses were addressed:

(1) Does the herb layer of the inactive floodplain differ from the active section?
  H1a: The species composition is different in the two floodplain sections.
  H1b: The plant community of the inactive floodplain has become a maple-ash forest.
(2) Do species of the active floodplain indicate more disturbance than plants of the inactive section?
  H2: The active floodplain has more Ellenberg indicator species for flooding, lower vegetation height (on-site measured height of the herbaceous layer), lower plant height at maturity (values from database) and lower seed mass.
(3) Do the active and inactive floodplain have different growth conditions?
  H3a: The herb layer in both sections has similar Ellenberg values for moisture and nutrient as well as a similar leaf dry matter content.
  H3b: The inactive section has fewer Ellenberg indicator species for periodical wet conditions.

2. Material and methods

2.1 Study area

The study was done within the ‘Schnalzaue’ near Peiting, southern Bavaria, Germany (WGS84 (lat/lon): 47.77406; 10.95948; 639 m a.s.l; Fig. 1). The underlying bedrock are Tertiary calcareous sediments on which nutrient-rich Calcaric Fluvisols have developed (LDBV 2017). The climate is temperate and suboceanic with a mean annual temperature of 7–8 °C (LfU 2017a) and mean annual rainfall of 1,100–1,300 mm (LfU 2017b) with a maximum in summer (MERKEL 2015). The course of the River Ammer is hardly modified and the previously mentioned weir is the only one at the river. The weir is located in the middle of the study area (river km 150.2–151.3; weir at km 150.7). The River Ammer has an alpine discharge pattern with summer floods (POTTGIESSER & SOMMERHÄUSER 2014), and an annual mean discharge of ca. 9 $m^3 s^{-1}$ (LfU 2013). The flanking alluvial forest is mainly formed by grey alder, ash and (planted) spruce.

2.2 Study design

Vegetation surveys, consisting of six plots in each floodplain section (plot area: 10 m × 10 m, separated by >24 m, parallel to the river) and following BRAUN-BLANQUET (1964), were conducted in June and July 2017 (Table 1). A semiquantitative scale from PFADENHAUER et al. (1986) was used to determine species cover; an area of 100 m^2 corresponded to minimum plot size for investigations of forest undergrowth (MÜLLER-DOMBOIS & ELLENBERG 1974). The study design captured only the vascular plant species of the herbaceous layer, while significant effects through light conditions of higher layers were statistically proved and excluded. Furthermore, the number of plots was limited by the length of the dam and adjacent forest plantation that were excluded. The spatial set-up of the plots in the active floodplain were similar to those in the inactive floodplain to avoid effects of distance to the weir (Fig. 1).

Nomenclature of plant species followed the ‘Plant List’ (www.theplantlist.org, accessed 14.07.2017) completed by JÄGER (2011) in case of inconclusive information; the nomenclature of plant communities was based on ‘FloraWeb’ (BfN 2018). The character species of the syntaxonomic units and indicator values were taken from ELLENBERG et al. (2001). For the analysis of functional plant traits, data for 76 of 97 herbaceous species were available from the ‘LEDA Traitbase’ (KLEYER et al. 2008). Databases were used because they correlate with field data and maintain the species hierarchy (KAZAKOU et al. 2014), since the interspecific variation of functional plant traits is normally larger than the intraspecific one (GARNIER et al. 2001, WRIGHT et al. 2004).

Table 1. GPS data for the twelve plots (additional map of Fig. 1). The coordinates are in the middle of the 100 m² plots.

Tabelle 1. GPS-Daten der zwölf Plots (zusätzlich Karte Abb. 1). Die Koordinaten markieren die Mitte der 100-m²-Plots.

Plot-ID	Floodplain	Weir	Distance to weir [m]	Position	Lat (WGS84)	Lon (WGS84)
IN1	Inactive	Above	205	Behind dam	47.7738	10.9566
IN2	Inactive	Above	239	Behind dam	47.7737	10.9562
IN3	Inactive	Above	273	Behind dam	47.7736	10.9558
IN4	Inactive	Above	353	Behind dam	47.7732	10.9548
IN5	Inactive	Above	387	Behind dam	47.7731	10.9546
IN6	Inactive	Above	421	Behind dam	47.7727	10.9544
AC1	Active	Below	205	No dam	47.7744	10.9622
AC2	Active	Below	239	No dam	47.7743	10.9627
AC3	Active	Below	273	No dam	47.7742	10.9632
AC4	Active	Below	380	No dam	47.7742	10.9640
AC5	Active	Below	414	No dam	47.7743	10.9644
AC6	Active	Below	448	No dam	47.7743	10.9649

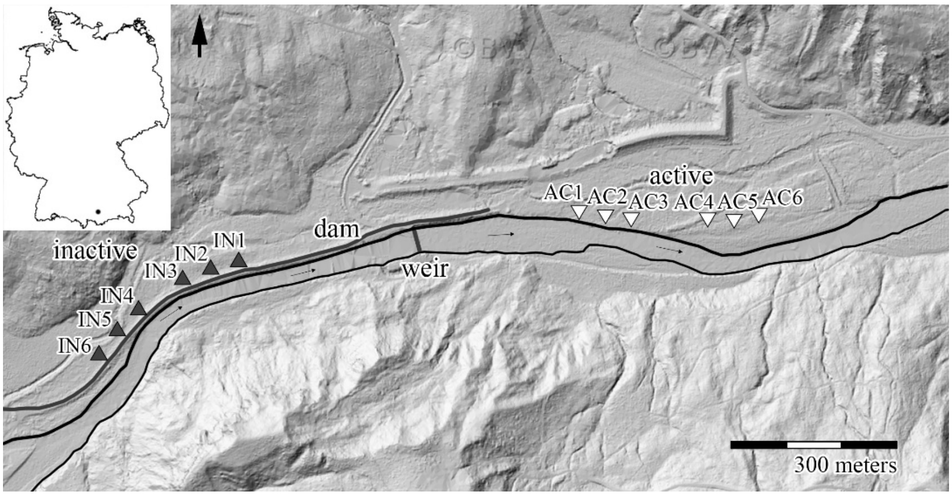

Fig. 1. The black dot marks the study site. It is located in the Alpine foreland on the River Ammer. The map shows the weir in the middle. From the weir 600 m westwards, a dam accompanies the River Ammer on the north. Six plots are located behind the dam above the weir in the inactive floodplain (grey triangles) and six plots are downstream the weir in the active floodplain (white triangles) (Terrain model: Geobasisdaten © Bayerische Vermessungsverwaltung).

Abb. 1. Der schwarze Punkt markiert das Untersuchungsgebiet. Es befindet sich im Alpenvorland an der Ammer. In der Mitte der Karte befindet sich das Schnalzwehr. Von dem Wehr 600 m Richtung Westen verläuft ein Damm entlang der Nordseite der Ammer. Sechs Aufnahmen wurden hinter dem Damm oberhalb vom Wehr in der inaktiven Aue durchgeführt (graue Dreiecke) und sechs Aufnahmen flussabwärts vom Wehr in der aktiven Aue (weiße Dreiecke) (Geländemodell: Geobasisdaten © Bayerische Vermessungsverwaltung).

2.3 Data analysis

Abundances of different syntaxonomic units were analysed by using descriptive methods. For each syntaxonomic level, abundances of the target character species were compared to abundances of character species from other units of the same syntaxonomic level. Ellenberg indicator values were evaluated descriptively, too. Therefore, the values were standardized by dividing the sum of all indicator species from each plot by the total number of species from the respective floodplain section.

The univariate statistics included analyses of average vegetation height, number of indicator species for flood, as well as periodical wet conditions and functional plant traits. In case of the analysis of functional plant traits, only herbaceous species were involved because their life form correlates with seed mass (MOLES et al. 2005) as well as with height; the reduction of layers was also stated by LAVERGNE et al. (2003). All values of functional plant traits were logarithmised. 'Community weighted means' (CWM) were calculated as:

$$CWM = \sum_{i=1}^{n} p_i \times trait_i$$

where

n = number of species;
p_i = abundance of species i;
$trait_i$ = value of functional plant trait; LAVOREL et al. 2008)

CWM was augmented by the 'functional dispersion' (FDis), which is defined by LALIBERTÉ & LEGENDRE (2010) as the abundance-weighted mean distance of single species to the weighted community centroid in multidimensional functional trait space. The number of dimensions arise from the number of used functional plant traits:

$$FDis = \frac{\sum a_j z_j}{\sum a_j}$$

where

a_j = abundance of species j;
z_j = distance of species j to centroid of all species

CWM values represent the respective optimum of a functional plant trait for specific environmental conditions and allow a verification, if there is a shifting in the traits in reaction to the presence of dam and weir. The FDis measures the dispersion of a functional plant trait within a plant community. Accordingly, a small FDis means that the species of a community are very similar to the respective functional plant trait and that there are strong habitat filters (CORNWELL et al. 2006).

For continuous independent variables (average vegetation height, functional plant traits) standard distribution was verified by Q–Q plots and variance homogeneity by Bartlett tests. If possible, ANOVAs, or alternatively, Kruskal-Wallis tests were calculated. In case of significant differences, Cohen's d and Pearson's correlation coefficient r were used. For numeric data (indicator species for flood and periodical wet conditions) generalized linear models with a Poisson distribution were calculated.

The variation in species composition between and within the floodplain sections was analysed by a NMDS ordination (non-metric multidimensional scaling) based on Bray-Curtis dissimilarities. The data were not transformed, although a transformation is recommended for improving the ordination (LEGENDRE & GALLAGHER 2001), resulting in reduced influence of species with high abundances. However, the latter is more important, because dominant species are the ones shaping ecosystem processes (GRIME 1974, GOLODETS et al. 2009). After proving the homogeneity of variances, significant differences in species composition between floodplain sections were verified by PERMANOVAs (permutional multivariate analysis of variance; ANDERSON 2001, MCARDLE & ANDERSON 2001) based on Bray-Curtis dissimilarities. *P* values are based on 999 permutations and corrections of multiple comparisons (BENJAMINI & HOCHBERG 1995). Ordination was overlapped by linear variables based on

999 permutations. The ordination included 114 species (inactive section 63, active 75, among invasive species *Impatiens glandulifera* and *Solidago gigantea*), with a stress of 0.12 (Fig. 2). Accordingly, the results seem reliable, while plot details should be neglected (LEYER & WESCHE 2007). All statistical analyses were done in R, Version 3.3.4 (R CORE TEAM 2017) and with the packages 'vegan' for the NMDS ordination (OKSANEN et al. 2017), and 'FD' to calculate CWM and FDis (LALIBERTÉ & LEGENDRE 2010).

3. Results

3.1 Species composition

The NMDS ordination of species composition showed significant differentiation between the active and inactive floodplain ($F_{1,10}$ = 5.13, p = 0.007; Fig. 2). The correlated environmental variables 'tree coverage' (R^2 = 0.29, p = 0.004) and 'average vegetation height' (R^2 = 0.37, p = 0.002) formed a significant gradient in the ordination diagram albeit orthogonal to the different species compositions of the active and inactive section (Fig. 2). Therefore, this gradient does not correspond to the differences between both sections, nor does distance of the plot to the weir explain the differences (R^2 = 0.20, p = 0.35; Fig. 2). We also examined if other correlated indicators would explain the differences between the sections.

In the active and inactive floodplain, the character species of the class *Querco-Fagetea* and the order *Fagetalia* dominated. Plant species of other classes or orders within the same formation or class had lower cover ratios (Fig. 3, Table 2). In the inactive floodplain, species of the alliance *Alno-Ulmion* dominated albeit not in the active floodplain. There, character species of *Fagion sylvaticae* Luquet 1926 (*Cardamine trifolia*) and *Carpinion betuli* Issler 1931 (*Vinca minor*) achieved together similar cover ratios as *Alno-Ulmion* character species. As the association *Alnetum incanae* and *Adoxo-Aceretum* have no specific character species within the herb layer (MÜLLER 1992, SEIBERT 1992), we had to focus on the tree layer and differential species. In both floodplain sections, (i) *Alnus incana* and *Fraxinus excelsior* co-dominated the tree layer; (ii) shrub coverage was on average 20%; (iii) no *Sambucus nigra* was found which would indicate a transition from *Alnetum incanae* to *Adoxo-Aceretum* (PFADENHAUER 1969); (iv) no differential species of *Tilio-Acerion to Alno-Ulmion* were present (*Geranium robertianum*; *Ribes uva-crispa*; MÜLLER 1992); (v) no character species of *Tilio-Acerion* were present; and (vi) *Asarum europaeum* grew in all but one plot.

Table 2. Character species of the target vegetation for the respective entities of phytosociology in the active and inactive floodplain. 'Character species of other syntaxa' depend on the same formation, class, order, alliance of the target vegetation, respectively.

Tabelle 2. Auflistung der Anzahl von Kennarten der jeweiligen pflanzensoziologischen Einheiten in Abhängigkeit der zwei Standorttypen ‚Charakterarten anderer Syntaxa' beziehen sich immer auf dieselbe Formation, Klasse, Ordnung bzw. Verband der Zielvegetation.

	Target vegetation	Inactive floodplain		Active floodplain	
		Character species	Character species of other syntaxa	Character species	Character species of other syntaxa
Class	*Querco-Fagetea*	21	0	23	2
Order	*Fagetalia sylvaticae*	16	0	18	1
Alliance	*Alno-Ulmion minoris*	5	1	6	2
Association	*Alnetum incanae*	1	0	1	1

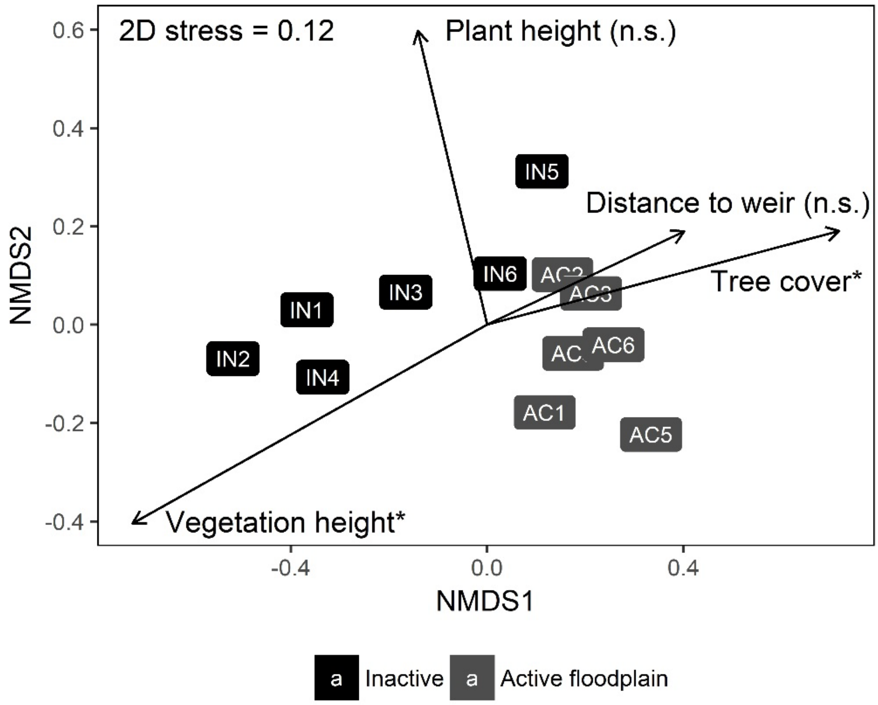

Fig. 2. NMDS ordination (non-metric multidimensional scaling) of the species composition in 12 plots on the River Ammer. 'Inactive' denotes the floodplain behind the dam above the weir and 'active' the floodplain below the weir without a dam. 'AC1' and 'IN1' are closest to the weir and similar far away. The environmental variables 'average vegetation height' (on-site measured height of herbaceous layer; $R^2 = 0.37$, $p = 0.002$) and 'tree coverage' ($R^2 = 0.29$, $p = 0.004$) are significant, 'plant height' (height at maturity of every species, values from 'LEDA Traitbase'; $R^2 = 0.10$, $p = 0.384$) and 'distance to weir' ($R^2 = 0.20$, $p = 0.353$) not. Significance level was $p < 0.05$. Ordination was calculated with Bray-Curtis dissimilarities; stress (based on two dimensions): 0.12.

Abb. 2. NMDS-Ordination (non-metric multidimensional scaling) der Artenzusammensetzung von den 12 Aufnahmeflächen. ‚Inactive' bezeichnet die Aue hinter dem Damm oberhalb vom Wehr und ‚active' die Aue unterhalb vom Wehr ohne Damm. ‚AC1' und ‚IN1' sind am nächsten am Wehr gelegen und gleich weit weg vom Wehr aber oberhalb bzw. unterhalb davon gelegen. Die Umweltvariablen mittlere Vegetationshöhe der Krautschicht ($R^2 = 0{,}37$; $p = 0{,}002$) und Baumdeckung ($R^2 = 0{,}29$; $p = 0{,}004$) sind signifikant, artspezifische Pflanzenhöhe zur Reifephase (‚plant height', Daten von ‚LEDA Traitbase'; $R^2 = 0{,}10$; $p = 0{,}384$) und Abstand zum Wehr ($R^2 = 0{,}20$; $p = 0{,}353$) nicht. Das Signifikanzniveau lag bei $p < 0{,}05$. Abstandsmaß: Bray-Curtis. Stress, basierend auf zwei Dimensionen: 0,12.

3.2 Disturbance indicators

It was expected that the disturbance indicator plant height would explain the difference in species composition between the active and inactive floodplain, but this variable was not significant ($R^2 = 0.10$, $p = 0.38$; Fig. 2). Also, the number of flood indicators was not different between both floodplain sections ($z_{1,10} = 0.00$, $p = 1.00$; Fig. 4). Community-weighted means of seed mass were similar in both sections ($F_{1,10} = 2.98$, $p = 0.115$), while functional dispersion (FDis) was different ($F_{1,10} = 5.00$, $p = 0.049$, d = -1.36, $r = -0.56$) (Fig. 6, Table 3). The average vegetation height did not differ significantly between the sections

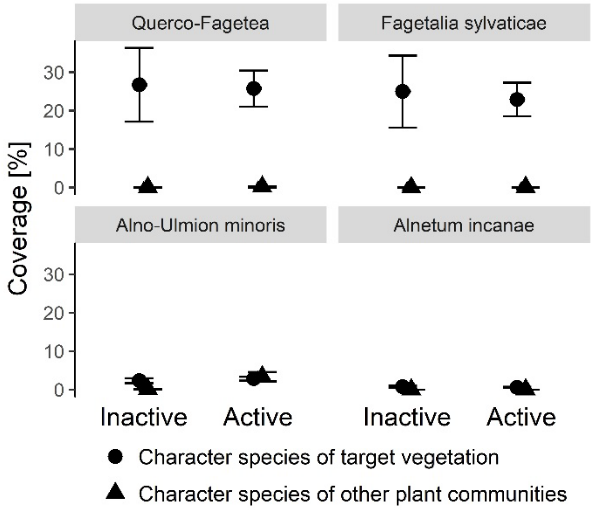

Fig. 3. Cover ratios of all character species of the target vegetation on all hierarchic levels (class, order, alliance, association) in contrast to the cover ratios of character species of other classes, orders, etc. within the same formation, class, etc. 'Inactive' denotes the floodplain behind the dam above the weir and 'active' the floodplain below the weir without a dam. The error bars show the standard error of the mean (SE).

Abb. 3. Deckungsgrade der Kennarten der Zielvegetation auf allen hierarchischen Ebenen (Klasse, Ordnung, Verband, Assoziation) im Vergleich zu den Deckungsgraden der Kennarten anderer Klassen, Ordnungen, etc. innerhalb derselben Formation, Klasse, etc. ‚Inactive' bezeichnet die Aue hinter dem Damm oberhalb vom Wehr und ‚active' die Aue unterhalb vom Wehr ohne Damm. Die Fehlerbalken entsprechen dem Standardfehler des Mittelwerts (SE).

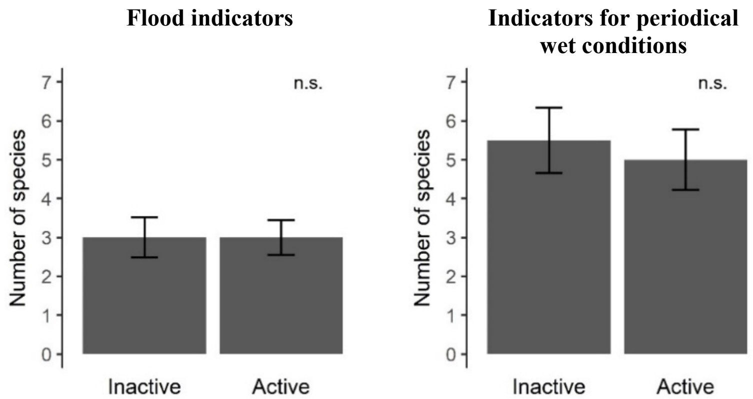

Fig. 4. Number of indicator species for floods and for periodically wet conditions according to ELLENBERG et al. (2001). 'Inactive' denotes the floodplain behind the dam above the weir and 'active' the floodplain below the weir without a dam. The error bars show the standard error of the mean (SE). Significance level was $p < 0.05$.

Abb. 4. Anzahl der Überflutungszeiger und Wechselfeuchtezeiger nach ELLENBERG et al. (2001). ‚Inactive' bezeichnet die Aue hinter dem Damm oberhalb vom Wehr und ‚active' die Aue unterhalb vom Wehr ohne Damm. Die Fehlerbalken entsprechen dem Standardfehler des Mittelwerts (SE). Das Signifikanzniveau lag bei $p < 0{,}05$.

Table 3. Average, not log-transformed community-weighted means (CWM) and average functional dipersions (FDis) of the herb layer from the active and inactive floodplain for the functional plant traits 'leaf dry matter content' (LDMC), 'seed mass', and plant height ('height at maturity'). Standard deviations (SD) are indicated and significant differences ($p < 0.05$) between bot floodplain parts are shown by asterisks (*).

Tabelle 3. Mittlere entlogarithmierte ‚community-weighted means' (CWM) und mittlere 'functional dispersions' (FDis) in den jeweiligen Standorttypen für die 'functional plant traits' Blattmasse-trockengehalt ('leaf dry matter content', LDMC), Samengewicht ('seed mass') und artspezifische Pflanzenhöhe ('height at maturity'). Es sind die Standardabweichungen (SD) angegeben und signifikante Unterschiede ($p < 0,05$) zwischen beiden Auenbereichen sind mit einem Sternchen markiert (*).

	Active floodplain	Inactive floodplain
CWM		
LDMC [mg g^{-1}]	232 ± 12	230 ± 15
Seed mass [mg]	1.04 ± 0.12	1.21 ± 0.21
Height at maturity* [m]	0.42 ± 0.03	0.50 ± 0.04
FDis		
LDMC	0.77 ± 0.06	0.86 ± 0.11
Seed mass*	0.76 ± 0.08	0.64 ± 0.10
Height at maturity	0.72 ± 0.08	0.79 ± 0.15

(active: 43.0 ± 5.2 cm, passive: 57.0 ± 16.3 cm, mean ± SD; $\chi^2(1) = 2.40$, $p = 0.121$). However, plant height was significantly lower in the active floodplain (CWM: $F_{1,10} = 13.6$, $p = 0.004$, d = 2.14, $r = 0.73$; Fig. 6, Table 3). Functional dispersion of plant height was not different between both floodplain sections ($\chi^2(1) = 0.23$, $p = 0.63$; Fig. 6).

3.3 Humidity and nutrient supply of the floodplain

Leaf dry matter content was similar at both the active and inactive floodplain (CWM: $F_{1,10} = 0.06$, $p = 0.810$; FDis: $F_{1,10} = 2.95$, $p = 0.12$; Fig. 6, Table 3). Equally, the number of indicators of periodically wet conditions was similar for both sections ($z_{1,10} = -0.38$, $p = 0.71$; Fig. 4). There were also no differences between the sections for the Ellenberg indicator values of moisture and nitrogen. The moisture values showed dominance of freshness (values 4–6) and wetness indicators (9). The nutrient value of 7 indicates nitrogen-rich substrate (Fig. 5).

4. Discussion

Overall, only slight differences in the forest vegetation between the active and inactive floodplain were observed after more than 50 years of separation by a dam. Only the ordination revealed differences between both floodplain sections but not the phytosociological analysis. All disturbance indicators showed no significant differences (flood indicators, vegetation height, seed mass), except height. There was no sign of a development towards a *Adoxo-Aceretum* in the inactive floodplain, while the *Alnetum incanae asaretosum* was present in both sections. This means that the alluvial forest is still a grey-alder forest with

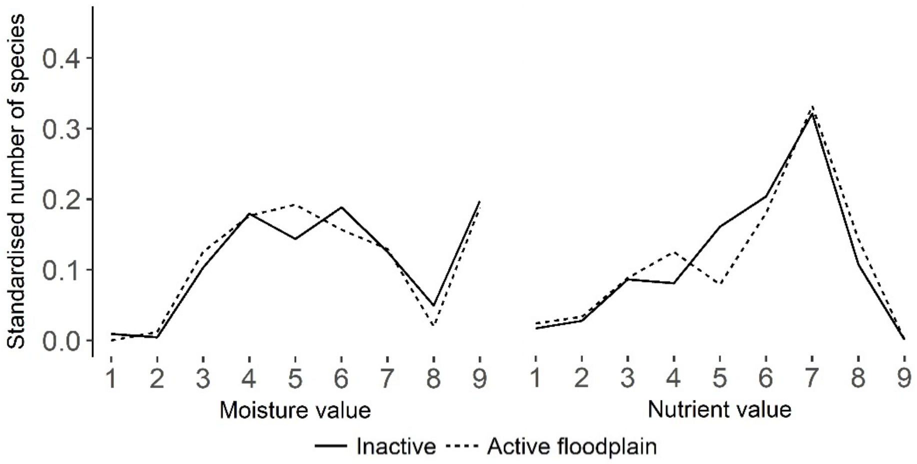

Fig. 5. Analysis of indicator values of ELLENBERG et al. (2001) for moisture and nitrogen indicated by standardised average species number. 'Inactive' denotes the floodplain behind the dam above the weir and 'active' the floodplain below the weir without a dam.

Abb. 5. Auswertung der Feuchte- und Stickstofftzahl nach ELLENBERG et al. (2001) durch Angabe der standardisierten mittleren Artenzahl. ‚Inactive' bezeichnet die Aue hinter dem Damm oberhalb vom Wehr und ‚active' die Aue unterhalb vom Wehr ohne Damm.

occasional flood events. This similarity of both floodplain sections is supported by similar indicator values for humidity and nutrient supply as indicated by LDMC, indicators of periodically wet conditions, and Ellenberg indicator values for moisture and nitrogen.

4.1 No development towards a *Adoxo-Aceretum* within the inactive floodplain

Thus, our first hypothesis (H1a) was confirmed by the ordination which revealed significant differences in the species composition of the active and inactive floodplain (Fig. 2). This is perfectly in line with a study also comparing a floodplain that had been inactive for 50 years within an active floodplain at River Elbe and River Weiße Elster in Central Germany (GLAESER & WULF 2009), and supports the results of a change in tree composition in inactive floodplains on River Rhine and River Wisconsin after more than 100 years (DEILLER et al. 2001, GERGEL et al. 2002).

On the contrary, the syntaxonomic analysis revealed no differences between both floodplain sections. Therefore, hypothesis H1b must be rejected, as there were no differential species within the *Adoxo-Aceretum* distinguishing it from the *Alnetum incanae*. The low presence of character species of *Alno-Ulmion* is untypical for *Alnetum incanae* (LEUSCHNER & ELLENBERG 2017; Table 2), as well as high shrub coverage (PFADENHAUER 1969, SCHWABE 1985). Nonetheless, the 20% shrub coverage in our study is not untypical for the submontane *Cornus sanguinea*-form of *Alnetum incane* as present within the study floodplain (SEIBERT 1992). Furthermore, the tree layer without dominant *Acer pseudoplatanus* and the herb layer with most indicators for *Alno-Ulmion* (Table 2) and without differential species of *Tilio-Acerion* suggest again the presence of the *Alnetum incanae asaretosum* in both floodplain sections, i.e., that there prevails a grey-alder forest with rare flood events (SCHWABE 1985). Indeed, the co-dominance of *Fraxinus excelsior* and *Alnus incana* is not typical for *Alnetum incanae* in the montane zone, while it is normal in the submontane zone

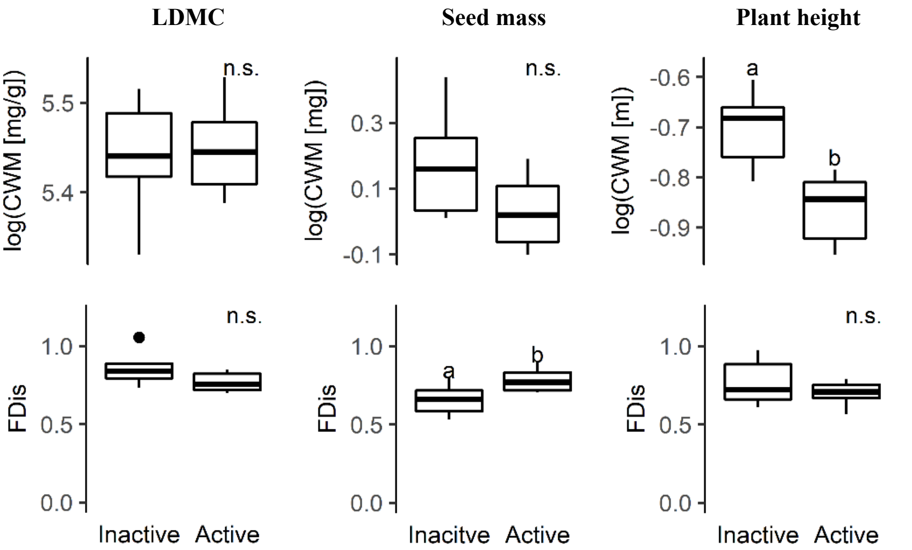

Fig. 6. Box-whisker plots of the community-weighted means (CWM) and the functional dispersions (FDis) for the functional plant traits 'leaf dry matter content' (LDMC), 'seed mass' and 'plant height'. 'Inactive' denotes the floodplain behind the dam above the weir and 'active' the floodplain below the weir without a dam. Significance differences ($p < 0.05$) were indicated with different letters. The not log-transformed values of the CWMs are in Table 3.

Abb. 6. ‚Box-whisker plots' der ‚community-weighted means' (CWM) und ‚functional dispersions' (FDis) für die funktionellen Pflanzeneigenschaften Blattmassetrockengehalt (‚leaf dry matter content', LDMC), Samengewicht (‚seed mass') und artspezifische Pflanzenhöhe (‚plant height'). ‚Inactive' bezeichnet die Aue hinter dem Damm oberhalb vom Wehr und ‚active' die Aue unterhalb vom Wehr ohne Damm. Signifikante Unterschiede ($p < 0,05$) sind mit unterschiedlichen Buchstaben markiert. Die entlogarithmieren Werte der CWMs befinden sich in Tabelle 3.

(SEIBERT 1992) where the study site is located. Combining the results of the ordination and the syntaxonomical analysis, we conclude that due to only marginal differences in site conditions, both floodplain sections can be considered equal in terms of their classification.

We can accept H3a, i.e., minor differences indicated by the ordination cannot be explained by Ellenberg values for moisture or nutrients since they are similar for both floodplain sections. Leaf dry matter content also indicated no significant differences between the sections. Thus, site conditions seem to be similar regarding water availability and nutrient supply (WILSON et al. 1999, CORNELISSEN et al. 2003). Thus, we have to reject H3b as there were no differences between both sections in Ellenberg species for periodical wet conditions.

4.2 The role of disturbance for differences in species composition

H2 was only partly confirmed, as the observations made for the environmental variable height indicate only small differences in vegetation structure between the active and inactive floodplain with a slightly more intense disturbance regime in the active section (Fig. 2). Conversely, the syntaxonomic result of an *Asarum*-subassociation of *Alnetum incanae* indicates a lack of disturbance in both sections. The latter is supported by equal numbers of flood-indicating species (Fig. 4).

The analysis of functional plant traits reveals that the indicator for temporal aspect of disturbance (e.g., height) is significantly lower in the active floodplain, resulting in more frequent disturbances than in the inactive floodplain (PÉREZ-HARGUINDEGUY et al. 2013) (Fig. 6). The indicator for the spatial aspect of disturbance 'seed mass' was not significantly different between both floodplain sections, but there was a tendency of lower seed mass in the active floodplain (Fig. 6), which fits to the interpretation of BAKER's (1972) data from California by WESTOBY et al. (1992). Larger seeds indicate poor dispersal abilities (WESTOBY et al. 2002), and most herbaceous forest species are actually poor dispersers with low diaspore production (HERMY et al. 1999). For this reason, the tendency of higher seed mass in the inactive floodplain is in line with the results of studies at River Elbe and River Meuse with more forest species in inactive compared with active floodplains (VAN LOOY et al. 2003, GLAESER & WULF 2009). Due to this plant trait, species composition in the inactive floodplain tend to change to more stress-tolerating forest vegetation which is less typical for alluvial forests (WESTOBY et al. 2002, GLAESER & WULF 2009). Average vegetation height does not seem to be a disturbance indicator; rather, it reflects a light gradient with increasing tree cover (Fig. 2).

Flood disturbance has three dimensions, i.e., intensity, frequency and timing (DEILLER et al. 2001, GLAESER & WULF 2009). However, timing cannot cause the lower 'height' value in the active floodplain because it is identical in both floodplain sections, whereas the dam induces differences in frequency and intensity. As there are annual flood events on alpine rivers, clear differences between the active and the protected inactive floodplain should be visible in the vegetation. Therefore, our observations indicate a low intense disturbance regime in the active floodplain in comparison to natural site conditions.

Low-water periods cannot be the reason as they have been similar since 1963 (LfU 2018). However, we observed high and steep embankments below the weir. This could be the result of self-deepening of the river which is typical below weirs due to higher erosion rates (DRESCHER 2016). River regulation has significant effects on vegetation (e.g., BEJARANO et al. 2018) for which height between floodplain and average water level is an important parameter (NILSSON et al. 1991). The assumption of low disturbance in both floodplain sections is underpinned by similar functional dispersion for all functional plant traits (0.76 ± 0.11; Fig. 6, Tabele 3). If functional dispersion had been somewhere lower, it would mean that it is a more important environmental filter for species (CORNWELL et al. 2006). However, functional dispersion of the disturbance indicator 'plant height' seems not to be more important than other functional plant traits, again pointing to low disturbance in the active floodplain. Although, functional dispersions are all in all similar, while the functional dispersion of seed mass is slightly but significant lower in the inactive floodplain. This means that filtering within the inactive, i.e., undisturbed, floodplain is stronger than filtering by disturbance in the active floodplain. This could also be explained by an extensive flood regime since this will lead to a rather intermediate disturbance regime which allows coexistence of species with smaller and bigger seeds. Lastly, as the vegetation structure is nearly similar in both floodplain sections, and only low disturbance is indicated by both, functional plant traits and vegetation types, we suggest that the weir affects the vegetation of the active floodplain in the same direction as the dam the vegetation of the inactive one.

4.3 Perspectives and implications for management

The study area is situated in a Special Area of Conservation (SAC) of the European Habitats Directive, namely 8331-302 ('Ammer vom Alpenrand bis zum NSG *Vogelfreistätte Ammersee-Südufer*'). This means that conservation measures have to be undertaken to protect the habitat type alluvial forests with *Alnus incana* (prioritised habitat type 91E0*). As the grey-alder forest in the whole floodplain appears in its rare flooded variant, the planned restoration will foster a development to a more disturbed subassociation 'typicum', thus maintaining this protected habitat. In addition, a restored floodplain will hamper the development of planted spruce stands which are undesired in this habitat type. A comparison of the results with a 'natural' reference at River Ammer was not possible due to a lack of such sites. Evidence-based river management requires long-term monitoring after restoration measures. Such monitoring can constantly guide to an 'adaptive restoration' strategy (HERRMANN & KOLLMANN 2015).

5. Conclusion

The study revealed only slight differences in vegetation structure between the active and inactive Schnalz floodplain after more than 50 years of separation. Beyond, the active floodplain hardly gave indications for disturbance. We state that the change of vegetation structure within an unflooded grey-alder forest is slow, as it is not accomplished witin half a century. Moreover, we assume that self-deepening of River Ammer below the weir reduced the flood regime in the active floodplain. For this reason, we would describe vegetation in both floodplain sections as *Alnetum incanae asaretosum*. The upcoming restoration will induce more dynamics to the entire floodplain, and this will foster the development to a more disturbed variant of *Alnetum incanae*. Additionally, analysing crucial functional plant traits (here the LHS scheme) turned out to be a useful tool to understand ecosystem states and processes. A long-term monitoring should be established to control the success of the restoration and to learn more about ecosystem processes in grey-alder forests.

Erweiterte deutsche Zusammenfassung

Einleitung – Heutzutage ist ein Großteil der alpinen Auen von technischen Wasserbaumaßnahmen stark beeinträchtigt. Unter anderem führen Wehre und Dämme zu weitreichenden Folgen für die hydromorphologische Dynamik der Flusssysteme (TOCKNER & STANFORD 2002), was wiederum Einflüsse auf die Auwaldvegetation hat (LEYER 2004). Die genauen Auswirkungen sind wenig untersucht, insbesondere diejenigen auf die Krautschicht der Auwälder (GLAESER & WULF 2009). Unsere Studie liefert neue Ergebnisse durch die Untersuchung der Auswirkungen eines Dammes und eines Wehres im Mittellauf der bayerischen Ammer und trägt somit zu einem besseren Verständnis der ökosystemaren Prozesse in Grauerlen-Auwäldern (*Alnetum incanae*) bei. Im Untersuchungsgebiet bewirken die Bauwerke seit 55 Jahren eine Aufteilung der Aue in einen aktiven Bereich, der nicht durch einen Damm abgetrennt ist, und einen inaktiven Bereich, der durch einen Damm abgetrennt ist (Abb. 1). Durch den Vergleich beider Bereiche sollten erwartete Unterschiede in deren Artenzusammensetzung kenntlich gemacht werden und deren Ursachen identifiziert werden.

Material und Methoden – Die Untersuchungen fanden im Juni und Juli 2017 in der ‚Schnalzaue' nahe Peiting, im Süden Bayerns/Deutschland statt (Flusskilometer 150,2–151,3; Wehr bei 150,7). Wir kombinierten einen pflanzensoziologischen Ansatz (Braun-Blanquet) mit einer Analyse funktioneller Pflanzeneigenschaften (WESTOBY 1998). Neben der Artenzusammensetzung und den funktionellen Pflanzeneigenschaften (‚functional plant traits': Blattmassetrockengehalt, Pflanzenhöhe bei Fruchtreife, Samengewicht) wurden Ellenberg-Indikatoren (Zeigerwerte für Stickstoff und Feuchte, Zeigerarten für Überschwemmung und Wechselfeuchte) und die mittlere Vegetationshöhe innerhalb der Plots ausgewertet. Die Auswertung beruht auf zwölf Vegetationsaufnahmen der Krautschicht (Plotgröße 10 m × 10 m, Mindestabstand 24 m, parallel zum Fluss angeordnet). Die Anordnung der Plots ist bezüglich der Distanz zum Wehr in beiden Bereichen ähnlich, um distanzabhängige Effekte zu vermeiden. Für die Analyse der funktionellen Pflanzeneigenschaften wurden die Daten der ‚LEDA Traitbase' verwendet (KLEYER et al. 2008).

Ergebnisse – Die Ordination zeigte für beide Auenbereiche unterschiedliche Artenzusammensetzungen ($F_{1,10}$ = 5,13; p = 0,007; Abb. 2), was durch die syntaxonomische Analyse jedoch nur schwach bestätigt wurde. Letztere deutet auf eine Subassoziation eines selten überfluteten Grauerlen-Auwaldes mit *Asarum europaeum* im gesamten Untersuchungsgebiet hin. In beiden Bereichen wurden ähnliche Bedingungen hinsichtlich der Feuchte- und Nährstoffverhältnisse vorgefunden. Demgegenüber indiziert einzig der Parameter Pflanzenhöhe etwas mehr Störung in der aktiven Aue (CWM: $F_{1,10}$ = 13,6; p = 0,004; d = 2,14; r = 0.73; Abb. 6; Tab. 3). Insgesamt legen die Ergebnisse wenig Störung in beiden Auenbereichen nahe.

Diskussion – Die Ordination zeigte signifikante Unterschiede in der Artenzusammensetzung zwischen aktiver und inaktiver Aue. Zu ähnlichen Ergebnissen kam eine Studie, welche ebenfalls eine 50 Jahre inaktive mit einer aktiven Aue an den Flüssen Elbe und Weiße Elster verglich (GLAESER & WULF 2009). Im Gegensatz dazu war keine Entwicklung zum Ahorn-Eschen-Wald (*Adoxo-Aceretum*) erkennbar, da die pflanzensoziologische Analyse keine Unterschiede zwischen den beiden Auen aufzeigte und keine Differentialarten des *Adoxo-Aceretum* eine Abgrenzung zum *Alnetum incanae* zuließen. Kombiniert man die Ordination mit der pflanzensoziologischen Auswertung, unterscheiden sich die beiden Auen in ihrer Artenzusammensetzung nur wenig. Diese Unterschiede zeigten sich nicht in den Ellenberg-Zeigerwerten für die Feuchtezahl und die Stickstoffzahl sowie den Blattmassetrockengehalt. Zudem bestätigte sich nicht, dass in der inaktiven Aue weniger Ellenberg-Zeigerarten für starke Wechsel der Feuchtigkeit vorhanden sind. Einen Rückschluss auf ein etwas ausgeprägteres Störungsregime in der aktiven Aue lässt nur die funktionelle Pflanzeneigenschaft der Pflanzenhöhe durch geringe signifikante Unterschiede zu (Abb. 2). Kontrovers dazu ist die pflanzensoziologische Zuordnung zum *Alnetum incanae asaretosum* anzusehen, welche einen Mangel an Störung in beiden Auen indiziert (vgl. SCHWABE 1985). Letzteres wird durch das Fehlen von Unterschieden in der Anzahl von Ellenberg-Überschwemmungszeigern unterstützt sowie von der Ähnlichkeit der ‚functional dispersions', d. h. ähnlich starke Umweltfilter aller untersuchten funktionellen Pflanzeneigenschaften (Abb. 6).

Schlussfolgerungen – Der Vergleich beider Auenabschnitte konnte den Effekt der Bauwerke auf die Krautschicht des örtlichen Grauerlen-Auwaldes aufzeigen und dient als Basis für ein zukünftiges Monitoring zu den Auswirkungen des Damm- und Wehrrückbaus im Zuge geplanter Renaturierungsmaßnahmen. Der Grund für das Ausbleiben größerer Unterschiede zwischen den beiden Auen bezüglich ihrer Artenzusammensetzung könnte die Selbsteintiefung der Ammer im Unterwasser des Wehres sein. Dies würde auch den dargelegten Mangel an Störung unterhalb des Wehres erklären. Da die Höhe zwischen Aue und mittlerem Wasserspiegel wesentlichen Einfluss auf die Vegetation hat (NILSSON et al. 1991), werden die Renaturierungsmaßnahmen die Flussdynamik im gesamten Auenbereich verbessern. Eine häufigere Störung der Vegetation wird somit der Erhaltung des Grauerlen-Auwaldes dienen.

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