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Functional plant traits as indicators of impacts on braided rivers

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Braided rivers are characterised by very high hydro- and morphodynamics. Human impacts altered the natural habitat structures and fluvial processes. In this work we examine to what extent habitat characteristics, species composition and functional plant traits are changed by river degradation. For this purpose, four river sections with different degrees of human impacts were investigated at the Upper Isar in Southern Germany: a diverted river section with bedload deficit, a near natural section, a regulated section and a restored section. In total, 31 habitat parameters and the cover of 19 typical floodplain species and their traits were investigated within 3 × 3 m plots. The plots were placed in different succession phases along three transects in each of the four sections. The statistical analysis was done using a median test. In addition, an evaluation of the relationships of traits with habitat parameters were performed via a NMDS (Non-metric Multidimensional Scaling). In summary, the results show that differently impacted river sections of braided rivers differ significantly in terms of habitat parameters, the occurrence and cover of section-specific plant species, as well as the plant traits. The results indicate that plant traits thus enable a superordinate analysis of human impacts on rivers.

Zittel A, Becker I, Kollmann J, Müller N, Egger G (2023) Funktionelle Pflanzenmerkmale als Indikatoren für Auswirkungen auf Umlagerungsflüsse.
Umlagerungsflüsse zeichnen sich durch eine sehr hohe Hydro- und Morphodynamik aus. Durch menschliche Eingriffe werden die natürlichen Habitatstrukturen und fluvialen Prozesse verändert. In dieser Arbeit wird untersucht, wie sich anthropogene Eingriffe auf die Standortfaktoren, die Artenzusammensetzung und funktionalen Pflanzenmerkmale auswirken. Dafür wurden an der Oberen Isar vier Flussabschnitte mit unterschiedlichen Eingriffen (Wasserausleitungsstrecke mit Geschiebedefizit, naturnaher Abschnitt, regulierter Abschnitt, renaturierter Abschnitt) untersucht. Es wurden 31 Standortfaktoren sowie die Deckungsgrade 19 auetypischer Pflanzenarten und deren funktionale Pflanzenmerkmale innerhalb von 3 × 3 m großen Aufnahmeflächen aufgenommen. Die Aufnahmeflächen wurden in den vier Abschnitten jeweils in drei Transekten in unterschiedliche Sukzessionsphasen gelegt. Die statistische Auswertung der Unterschiede der Abschnitte erfolgte über einen Median-Test. Weiters fand eine Auswertung der Zusammenhänge der Pflanzenmerkmale mit den Standortfaktoren über eine NMDS (Non-metric Multidimensional Scaling) statt. Die Ergebnisse zeigen, dass unterschiedlich degradierte Flussabschnitte von Umlagerungsflüssen sich durch die Standortsfaktoren, das Vorkommen und den Deckungsgrad abschnittsspezifischer Pflanzenarten sowie den Pflanzenmerkmalen signifikant unterscheiden. Weiters kann nachgewiesen werden, dass Pflanzenmerkmale eine umfassende Analyse der menschlichen Eingriffe in Flüsse ermöglichen.

Keywords: plant traits, Upper Isar, riparian restoration, human impact, water diversion.

Introduction

Gravel-bed rivers and particularly braided rivers are characterised by an exceptionally high diversity of habitats and highly specialized fauna and flora. Despite their great ecological value, they are among the most endangered ecosystems worldwide (Tockner & Stanford 2002; Hauer et al. 2016). In the European Alps the situation is even more critical, as due to systematic river regulations since the mid-19th century less than half of the braided river sections remain (15 % of formerly 34 %; Hohensinner et al. 2021; Müller 1995 b). Along

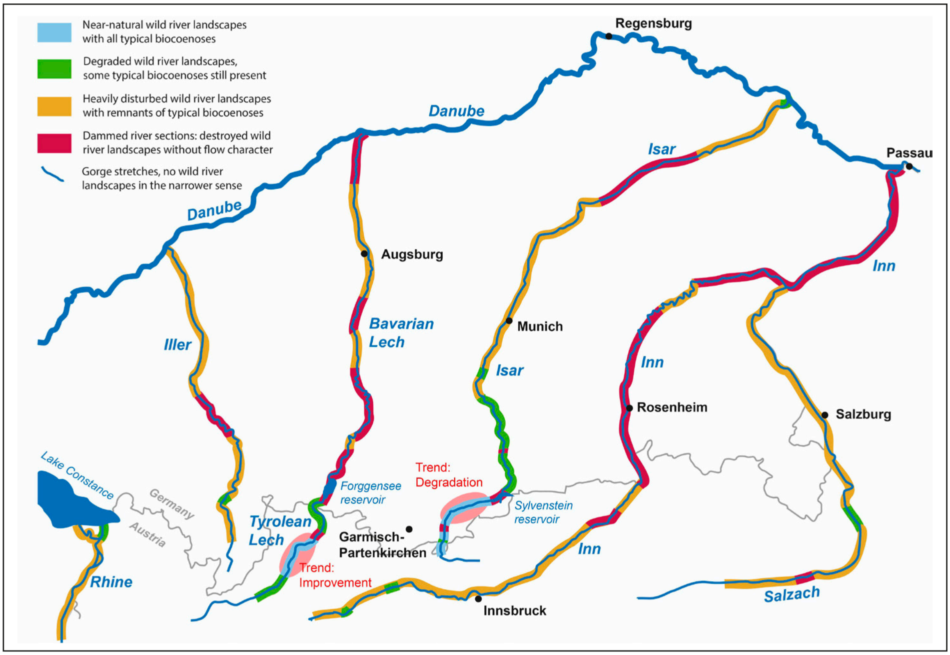


Fig. 1: Classification of the northern alpine wild river landscapes with four degrees of naturalness (after Müller 1991, updated from N. Müller in WWF Deutschland 2022). – Abb. 1: Klassifizierung der nordalpinen Wildflusslandschaften anhand von vier Natürlichkeitsgraden (nach Müller 1991, aktualisiert von N. Müller in WWF Deutschland 2022).

the northern alpine rivers only at the Tyrolean Lech in Austria and at the Upper Isar near-natural sections with all typical species and habitats persist (Fig. 1). Therefore, these last braided river courses are especially important as reference ecosystems for the implementation of the Natura 2000 Directive, EU Birds and Habitats Directives (92/43/EEC) and Water Framework Directive (2000/60/EC), and as species pools for river restoration.

Braided rivers represent extreme ecosystems due to their specific disturbance regime (Egger et al. 2022; Hohensinner et al. 2019). Only specifically adapted species can establish and survive here. Therefore, plants in braided rivers must have special traits which allow them to cope with frequent disturbance and stress (cf. Violle et al. 2007; Catford & Jansson 2014).

The fitness of the species is determined by their performance and their appearance in the habitat in terms of growth, reproduction and survival. These three properties, summarized as performance traits, are largely determined indirectly by the functional traits. These can be divided into phenological, morphological and physiological traits and can be measured at plant level (Violle et al. 2007). In case of changing environmental factors, it can be assumed that the traits change as well (McIntyre et al. 1999).

Different environmental conditions therefore determine the trait quality and the diversity of the traits. Thus, trait diversity reflects ecological selection within the ecosystem constituting specific plant communities. Competition, disturbance and harsh environmental conditions have an impact on both increasing and decreasing trait divergence (Richardson et al. 2012). In addition, with an ongoing succession the trait diversity generally decreases (Fukami et al. 2005; Roeder et al. 2012).

To date, functional traits were mostly used to characterize the succession phases found along rivers and to explain plant population factors to river dynamics (Corenblit et al. 2015, 2009). With the help of functional traits, a connection between changing environmental factors and vegetation can be established (Keddy 1992; McIntyre et al. 1999; Patten & Auble 1981). The functional plant traits in connection with the impacts on braided rivers were currently only considered to a small extent.

These functional characteristics in connection with the corresponding local habitat parameters as indicators of human impact are the focus of this study. The overall objective is to show the variation between different sections of the Upper Isar River, which are characterised by different impacts. Upstream of the Sylvenstein reservoir, the hydrodynamics and bedload transport in the diverted river section are reduced by the water diversion of the Isar and its tributaries for hydropower utilisation. This leads to a reduction of characteristic processes of wild river landscapes and consequently to an impoverishment of typical habitats and species. Nevertheless, the Upper Isar can be classified as a near-natural wild river landscape despite the diversion (Reich & Rethschulte 2021; Juszczyk et al. 2020). Downstream of the Sylvenstein reservoir, the river regulation and the construction of the reservoir have destroyed the wild river landscape (Maier et al. 2021). This leads to the following research questions (Zittel 2020):

How do the sections of the Upper Isar differ in terms of their habitat parameters, plant species and plant traits?

Are plant traits correlated with environmental factors?

Study site

The Upper Isar is defined as the river reach from the stream source in Tyrol (Austria) at an altitude of 1,200 m above sea level, to the confluence with the Loisach river. Until the 20th century, the Upper Isar was a wild landscape with an extensive braided floodplain (Müller 1995 a). Today, it is one of the last river sections with near-natural river reaches, but also includes sections with human impact and restoration. For these reasons, the Upper Isar was selected for this study.

The following study sections were chosen (Fig. 2):

- Section 1 extends from Wallgau to the mouth of the Rißbach (river km 247–236). It suffers from water diversion at the Krüner Weir and bed load management in the upstream section. The loss of dynamics in the gravel banks and river channels (Bayerisches Landesamt für Umwelt 2011) facilitates succession as shown by an increased cover of willow scrubs (Reich et al. 2008; Juszczyk et al. 2020). Moreover, the water deficit generates dry habitats (Poschlod 2016). However, the section has not been regulated and there is no bank protection.

- Section 2 extends from the mouth of the Rißbach to the Sylvenstein reservoir (river km 234–232). This is the most natural area of the Isar due to the high and natural bed load input of the Rißbach, despite the modification of the river in this area and water ab-

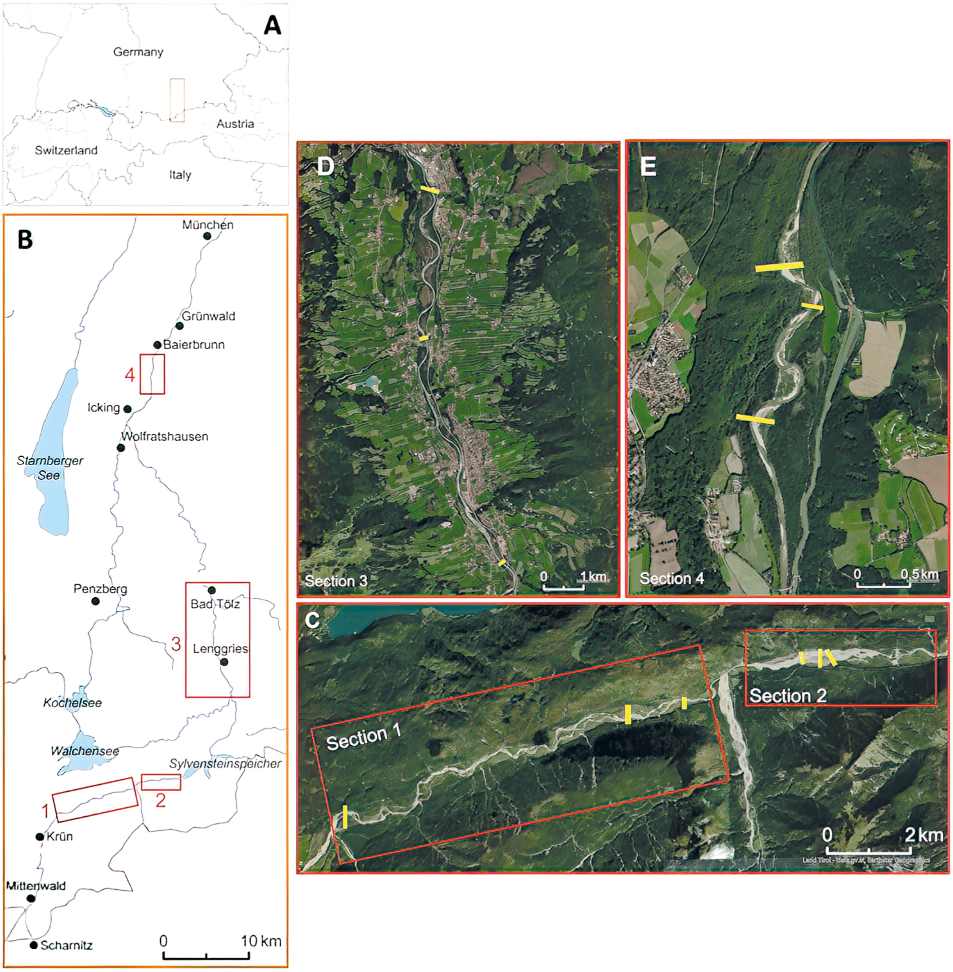


Fig. 2: Location of the Upper Isar (A) and the four river sections (B) in Southern Germany. The sections are shown by the red frames (C–E) with the location of the transects as red lines. (Google Maps 2019; modified from Zittel 2020) – Abb. 2: Lage der Oberen Isar (A) und der vier ausgewählten Abschnitte (B) in Süddeutschland. Zusätzlich ist die Lage der Transekte als rote Linien in den vier Flussabschnitten (rote Rechtecke, C–E) gekennzeichnet. (Google Maps 2019; verändert nach Zittel 2020).

straction from the Rißbach. Due to the nutrient-poor limestone gravel, vegetation-poor gravel banks and islands dominate the floodplain (Müller 1995 a, Bayerisches Landesamt für Umwelt 2011; Fig. 3). The dynamics of this section are similar to natural conditions of braided rivers, and are characterized by a mosaic of different types of vegetation (Schauer 1998; Juszczyk et al. 2020; Reich et al. 2008).

- Section 3 is located between Lenggries and Bad Tölz downstream of the Sylvenstein reservoir (river km 201–211). The section is regulated and impacted by dam operations (Speer 1977; Maier et al. 2021). In addition, due to the retention capacity of the Sylvenstein reservoir, there is a bed load deficit. The flood peaks are capped, which reduces the

Fig. 3: Aerial view of the near-natural river section 2 upstream of the Sylvenstein reservoir. The frequent high flood pulses with sediment load allows vegetation only to develop in patches on slightly higher areas (picture by G. Egger). – Abb. 3: Schrägluftbild des naturnahen Flussabschnitts 2 flussauf des Sylvensteinspeichers. Die regelmäßigen Hochwasser mit Geschiebetransport stören die Vegetationsentwicklung, die sich daher nur auf etwas höheren Bereichen ausbilden kann (Foto von G. Egger).

characteristic disturbance patterns. The Isar is restricted to one channel by bank structures (Hettrich & Ruff 2011) resulting in river bed depth erosion (Maier et al. 2021). The non-relocated gravel banks are often covered with dense vegetation (Bayerisches Landesamt für Umwelt 2011).

- Section 4 is located about 6 km downstream of the Loisach estuary near Schäftlarn at river km 165–158. The former regulated area was restored between 1999 and 2002. Riverbank stabilisations were removed, and the river received additional gravel and more water. Despite of the location of the restoration in a diverted river section, the flood dynamics are still effective. Due to this at least some of the former riparian forests have been eroded and new gravel banks developed (Muhar et al. 2019; Bayerisches Landesamt für Umwelt 2011).

Methods

Vegetation and habitat parameters

During the field work in June 2019, habitat parameters and vegetation traits were recorded using a scheme of individual plots along transects. The transects were arranged perpendicular to the course of the river (Fig. 4). Within each of the four sections, three randomly selected transects were chosen. Transect length always refers to the whole morphological floodplain including the fossil floodplain. Transects 1–3 belong to Section 1, 4–6 to Section 2, 7–9 to Section 3, and transects 10–12 to the restored Section 4.

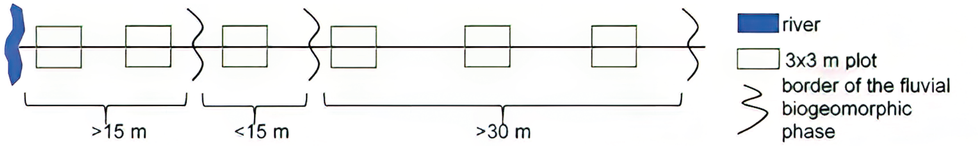


Fig. 4: Overview of the sampling design for the field work. Depending on the length of the fluvial succession phase (after Corenblit et al. 2007), different numbers of plots were set to cover all vegetation patterns. If the succession phase was <15 m in length, one plot was established; if the length was <30 m, two plots were placed; and if the length was ≥30 m, three plots were used (Zittel 2020). – Abb. 4: Überblick über das Aufnahmedesign der Geländearbeiten. Abhängig von der Länge der fluvialen Sukzessionsphase (nach Corenblit et al. 2007) wurde eine unterschiedliche Anzahl von Aufnahmeflächen angelegt, um alle Vegetationseinheiten abzudecken. Bei einer Länge der Sukzessionsphase von <15 m wurde eine Aufnahmefläche angelegt; bei einer Länge von <30 m wurden zwei Aufnahmeflächen angelegt; und bei einer Länge von ≥30 m drei Aufnahmeflächen (Zittel 2020).

Within the transects, 3 x 3 m plots were set randomly in each occurring fluvial biogeomorphic phase of Corenblit et al. (2007). Depending on the length of the biogeomorphic phases, different numbers of plots were set to cover all vegetation patterns (Fig. 4).

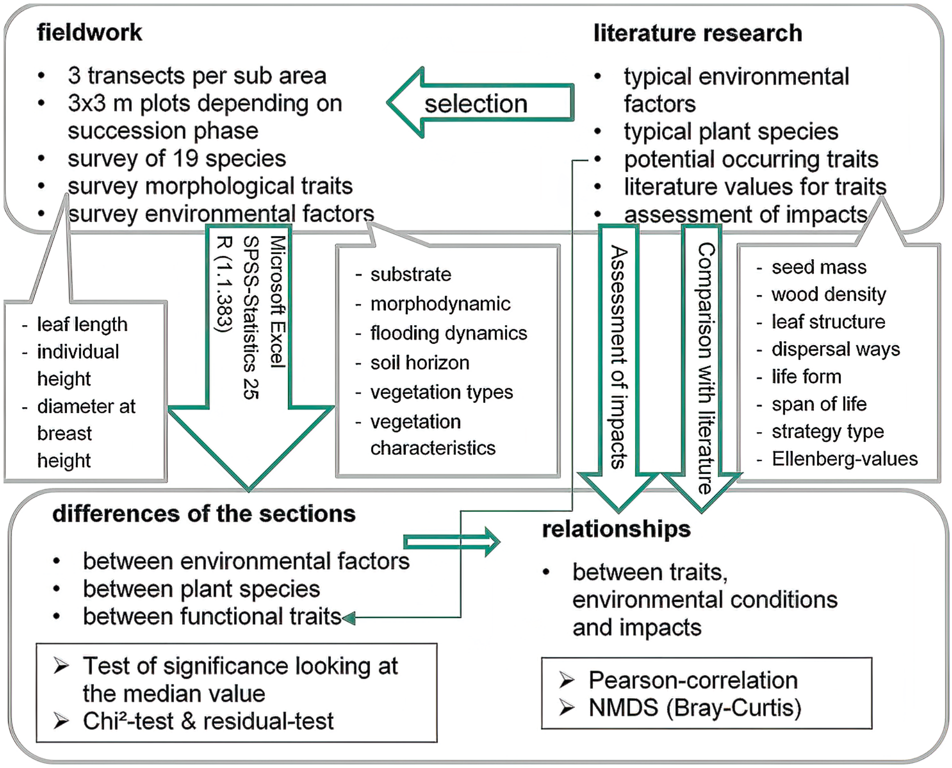


Fig. 5: Methodological approach and relationships of data evaluation (modified from Zittel 2020). – Abb. 5: Methodischer Ansatz und Zusammenhänge der Datenauswertung (verändert nach Zittel 2020).

Tab. 1: Parameters collected in the field and from literature (modified from Zittel 2020). – Tab. 1: Im Gelände und aus der Literatur erhobene Parameter (verändert nach Zittel 2020).

Environmental factors	**Vegetation characteristics**	**Selected plant species**	**Traits**
AB: cover bare soil [%] ASt: cover stones [%] ABl: cover rocks [%] Aki: cover gravel [%] ASa: cover sand [%] ASc: cover silt [%] Th: cover deadwood [%] StrD: cover litter [%] StrT: depth litter [cm] T_O: depth O horizon [cm] T_A: depth A horizon [cm] T_F: depth fine soil [cm] MK: morphodynamic GK: wood damage ÜK: flood dynamics CP: biogeomorphic succession after Corenblit et al. (2007)	B: canopy openness [%] Dg: total cover [%] DM: cover moss layer [%] DK: cover herb layer [%] DS: cover shrub layer [%] DB: cover tree layer [%] dHM: ∅ height moss l. [m] dHK: ∅ height herb l. [m] dHS: ∅ height shrub l. [m] dHB: ∅ height tree l. [m] mHK: max. height herb l. [m] mHS: max. height shrub l. [m] mHB: max. height tree l. [m] VR: vegetation type after Reich et al. (2008) VE: vegetation type after Egger et al. (2007)	*Acer pseudoplatanus* *Alnus incana* *Bromus erectus* *Calamagrostis pseudophragmites* *Chondrilla chondrilloides* *Dryas octopetala* *Erica carnea* *Fraxinus excelsior* *Impatiens glandulifera* *Juniperus communis* *Molinia caerulea* agg. *Myricaria germanica* *Petasites paradoxus* *Picea abies* *Pinus uncinata* *Pinus sylvestris* *Salix eleagnos* *Salix purpurea* *Solidago gigantea* *Solidago canadensis*	*Published data:* BA: leaf endurance BF: leaf form leaf anatomy X: xeromorphic form AF: expansion form seed dispersal SG: seed mass LF: life form ST: strategy type V: lignification HD: wood density span of life Ellenberg values *Field data:* dBl mean leaf length dH mean height dBHU mean range at breast height dBM biomass

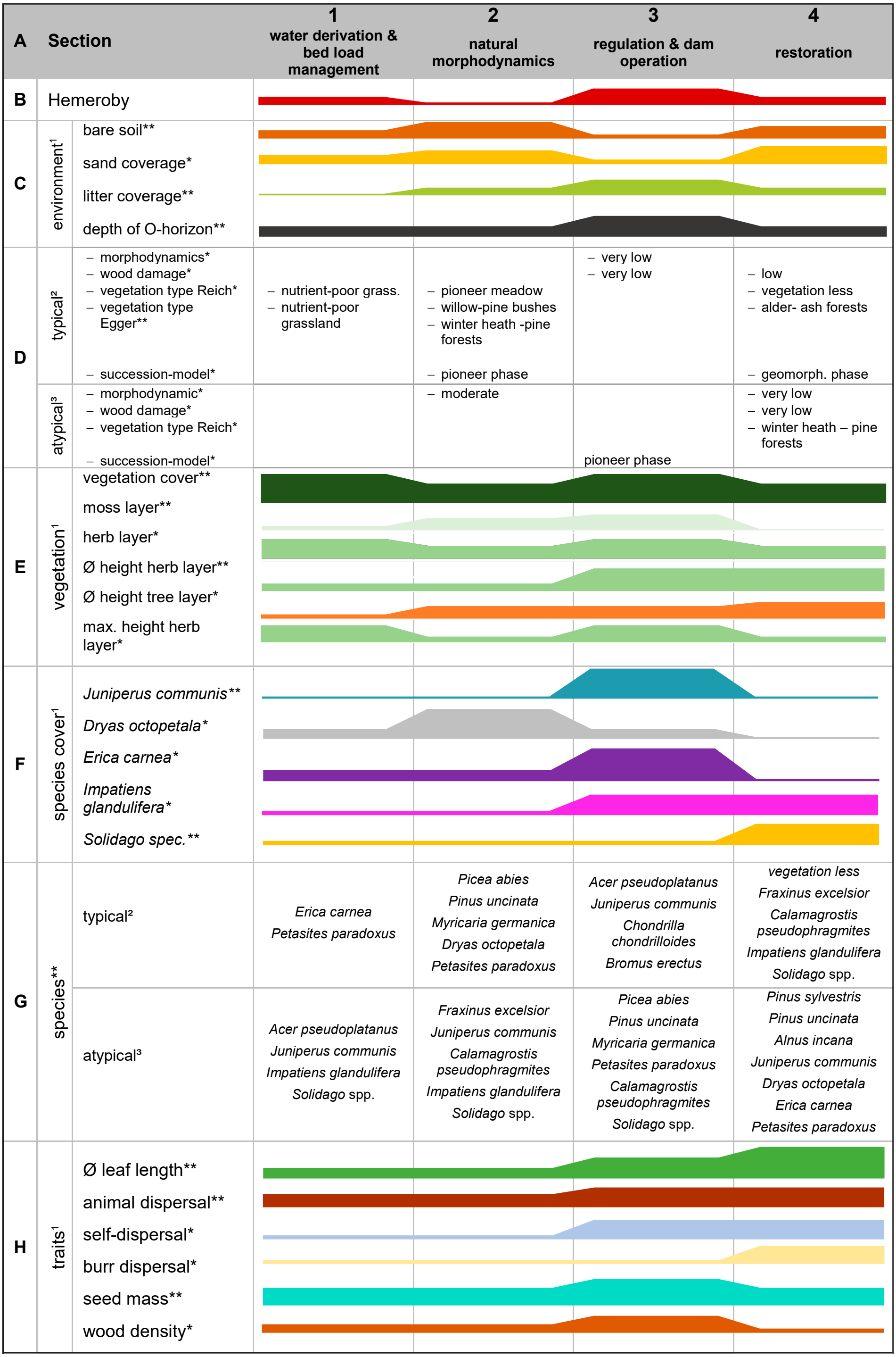
In total, 31 parameters were recorded for 86 plots (Tab. 1). In each plot the habitat parameters were gathered. Besides, 19 plant species were selected as typical species of each succession phase. The floristic determination was made according to Fischer et al. (2008). Their coverage, individual plant height, diameter at breast height (DBH), mean leaf length and plant traits were collected in the field. Additionally, plant traits and Ellenberg values (Ellenberg & Leuschner 2010) were collected from the literature (s. Zittel 2020; Fig. 5).

Statistical analysis

To test the differences between the sections, the metric habitat parameters, plant coverage and metric traits of the transects were statistically verified over the mean values. Therefore, the median test was used at the global level to check if there were statistically significant differences of the transects of the sections. The test result was considered significant for $p \leq 0.05$. If there were significant differences at the global level, we checked with post-hoc tests about the location of these differences at the local level.

The nonmetric environmental parameters, the occurrence of species and nonmetric traits were tested by a Chi^2-test at the global level and in a second step at the local level over residual tests, to check which attribute-composition was "typical" (statistically overrepresented) or "atypical" (statistically underrepresented) for the section. All combinations of characteristics in which the corrected residuals are $u [ij] > 1.96$, are referred to as typical and all combinations of characteristics with $u [ij] < -1.96$ as atypical.

The relationships of the traits and the environmental parameters were made visible with a Pearson-correlation and in a NMDS (Non-metric Multidimensional Scaling) using the Bray-Curtis distance measure.



A	Section		1 water derivation & bed load management	2 natural morphodynamics	3 regulation & dam operation	4 restoration
B	Hemeroby					
C	environment¹	bare soil**				
		sand coverage*				
		litter coverage**				
		depth of O-horizon**				
D	typical²	– morphodynamics*			– very low	
		– wood damage*			– very low	– low
		– vegetation type Reich*	– nutrient-poor grass.	– pioneer meadow		– vegetation less
		– vegetation type Egger**	– nutrient-poor grassland	– willow-pine bushes – winter heath -pine forests		– alder- ash forests
		– succession-model*		– pioneer phase		– geomorph. phase
	atypical³	– morphodynamic*		– moderate		– very low
		– wood damage*				– very low
		– vegetation type Reich*				– winter heath – pine forests
		– succession-model*			pioneer phase	
E	vegetation¹	vegetation cover**				
		moss layer**				
		herb layer*				
		Ø height herb layer**				
		Ø height tree layer*				
		max. height herb layer*				
F	species cover¹	*Juniperus communis***				
		*Dryas octopetala**				
		*Erica carnea**				
		*Impatiens glandulifera**				
		*Solidago spec.***				
G	species**	typical²	*Erica carnea* *Petasites paradoxus*	*Picea abies* *Pinus uncinata* *Myricaria germanica* *Dryas octopetala* *Petasites paradoxus*	*Acer pseudoplatanus* *Juniperus communis* *Chondrilla chondrilloides* *Bromus erectus*	*vegetation less* *Fraxinus excelsior* *Calamagrostis pseudophragmites* *Impatiens glandulifera* *Solidago* spp.
		atypical³	*Acer pseudoplatanus* *Juniperus communis* *Impatiens glandulifera* *Solidago* spp.	*Fraxinus excelsior* *Juniperus communis* *Calamagrostis pseudophragmites* *Impatiens glandulifera* *Solidago* spp.	*Picea abies* *Pinus uncinata* *Myricaria germanica* *Petasites paradoxus* *Calamagrostis pseudophragmites* *Solidago* spp.	*Pinus sylvestris* *Pinus uncinata* *Alnus incana* *Juniperus communis* *Dryas octopetala* *Erica carnea* *Petasites paradoxus*
H	traits¹	Ø leaf length**				
		animal dispersal**				
		self-dispersal*				
		burr dispersal*				
		seed mass**				
		wood density*				

A	Section		1 water derivation & bed load management	2 natural morphodynamics	3 regulation & dam operation	4 restoration
I	typical^2	– leaf endurance**		– evergreen		– deciduous- + overwinter green
		– life form**				– therophyte, geophyte
		– strategy type*		– stress tolerant		– competitor-ruderal
		– xeromorphic form*			– evasive	– enduring
		– Ellenberg values L T K F R N S	– x 3 x x x 4 x	– x 3 5 6 x 4 x	– x 2 x 4 x 3/5 x	– x 6 7 8 9 5/7 x
	atypical^3	– leaf endurance**				– evergreen
		– life form**			– geophyte	– chamaephyte
		– xeromorphic form*			– enduring	– evasive
		– Ellenberg values – L T K F R N S		– x x 3 x x x x	– x 3 x x x 4 x	– x x x 4 8 2 x

Fig. 6: Summary of the results showing differences between the four river sections at the Upper Isar: **A** the sections with their main impacts; **B** the hemeroby of the sections; **C**, **D** and **E** the differences of the environmental factors between the sections, using the median, with **C** metric , **D** nonmetric values and **E** metric vegetation attributes. **F** presents the differences in species cover, and **G** the typical and atypical plants for each section; **H** shows the metrical traits, and **I** the nonmetric traits. *: $0.05 > p > 0.01$; **: $p < 0.01$; ^{1}: tested by median test; ^{2}: tested by residual test with u[ij] > 1.96; ^{3}: tested by residual test with u[ij] < –1.96 (modified from Zittel 2020). – Abb. 6: Übersicht der Ergebnisse, welche die Unterschiede zwischen den Abschnitten der Oberen Isar zeigen: **A** die Abschnitte mit ihren Haupteingriffen, **B** die Hemerobie der Teilbereiche; **C**, **D** und **E** die Unterschiede der Umweltfaktoren zwischen den Abschnitten, dargestellt anhand des Medians: **C** metrische Werte, **D** nicht-metrische Werte und **E** metrische Vegetationsattribute. **F** zeigt die Unterschiede in der Artenvielfalt und **G** die typischen und atypischen Pflanzen für jeden Abschnitt. **H** zeigt die metrischen Merkmale und **I** die nicht-metrischen Pflanzenmerkmale. *: 0,05 > p > 0,01; **: p < 0,01; 1: getestet durch Median-Test; 2: getestet durch Residual-Test mit u[ij] > 1,96; 3: getestet durch Residual-Test mit u[ij] < –1,96 (verändert aus Zittel 2020).

Results

Differences of habitat parameters

The median test pointed out that 15 out of 31 variables showed statistically significant differences among the four sections (Fig. 6 C, D, E). The part of bare soil was highest in the near-natural Section 2, followed by the restored Section 4, whereas the cover of litter was highest in the regulated Section 3. The depth of the O-horizon, the vegetation cover, cover of moss and herb layer as well as the maximum tree height were highest in the regulated Section 3.

Differences of plant species

Regarding the species coverage in the plots, five out of 19 species showed statistically significant differences between the sections with the median test. *Juniperus communis* was only found in the regulated Section 3, the highest coverage of *Erica carnea* was also in Section 3, whereas *Dryas octopetala* showed its highest coverage in the near-natural Section 2. The alien plant species *Impatiens glandulifera* and *Solidago* spec. were only represented in the regulated and the restored Sections 3 and 4. Looking at the occurrence of species in the sections, over- and underrepresented species were found at all sections (Fig. 5, part G).

Differences of traits

Ten of the considered traits and five Ellenberg values showed statistically significant differences among the sections. Leaf length was highest in regulated Section 3 and restored

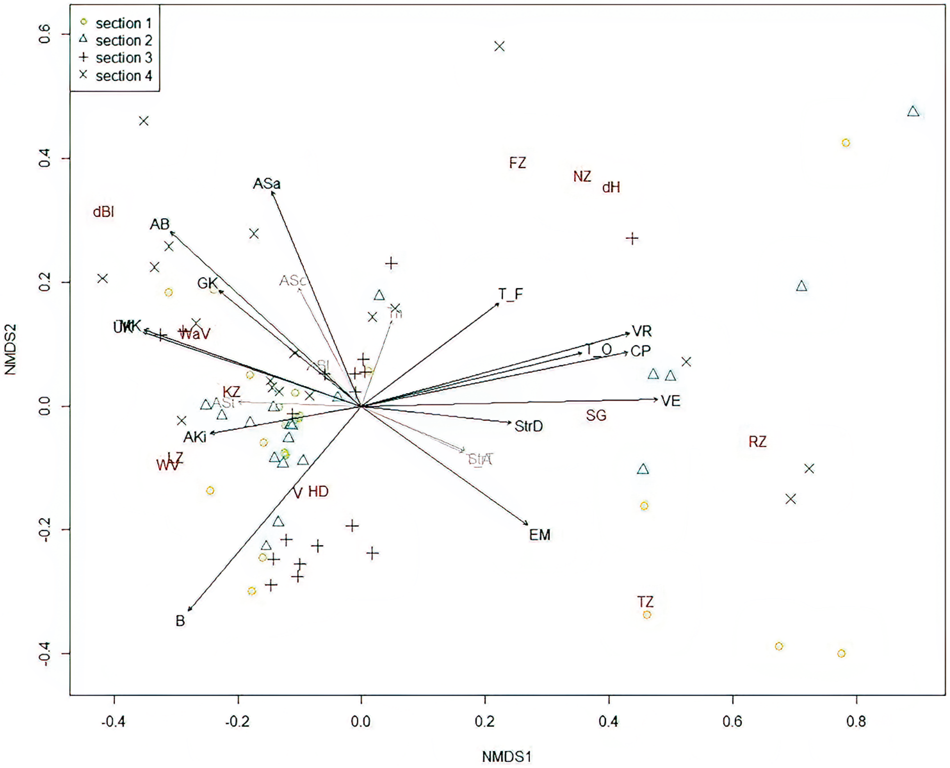


Fig. 7: Non-metric Multidimensional Scaling (NMDS) of the plot ordination looking at traits across all sections (dBl = mean leaf length, WaV = water dispersal, KZ = continentality value, LZ = light value, WV = wind dispersal, V = lignification, HD = wood density, FZ = humidity value, NZ = nitrogen value, dH = mean height, SG = seed mass, RZ = acidity value, TZ = temperature value). Additionally, environmental factors were added to the NMDS (ASa = cover of sand, AB = cover of bare soil, ASc = cover of silt, GK = wood damage, MK = morphodynamic, ÜK = flood dynamic, ASt = stone cover, Aki = gravel cover, B = canopy openness, EM = distance to mean water, T_A = depth of A-horizon, Str = litter depth, StrD = litter cover, T_O = depth O-horizon, T_F = depth of fine soil, Th = deadwood cover , VE = vegetation type after Egger et al. (2007), VR = vegetation type after Reich et al. (2008), CP = biogeomorphic succession phase after Corenblit et al. (2007). The environmental factors (black font) show statistically significant relationships (modified from Zittel 2020). – Abb. 7: Nicht-metrische multidimensionale Skalierung (NMDS) der Plot-Ordination unter Berücksichtigung von Pflanzenmerkmalen über alle Abschnitte (dBl = mittlere Blattlänge, WaV = Wasserausbreitung, KZ = Kontinentalitätswert, LZ = Lichtwert, WV = Windausbreitung, V = Verholzung, HD = Holzdichte, FZ = Feuchtezahl, NZ = Stickstoffzahl, dH = mittlere Höhe, SG = Samenmasse, RZ = Reaktionszahl, TZ = Temperaturzahl). Zusätzlich wurden dem NMDS Umweltfaktoren hinzugefügt (ASa = Anteil Sand, AB = Anteil offener Boden, ASc = Anteil Schluff, GK = Holzschäden, MK = Morphodynamik, ÜK = Hochwasserdynamik, ASt = Anteil Steine, Aki = Anteil Kies, B = Offenheit des Kronendachs, EM = Abstand zum Mittelwasser, T_A = Mächtigkeit A-Horizont, Str = Mächtigkeit Streu, StrD = Anteil Streubedeckung, T_O = Mächtigkeit O-Horizont, T_F = Mächtigkeit Feinboden, Th = Anteil Totholzbedeckung, VE = Vegetationstyp nach Egger et al. (2007), VR = Vegetationstyp nach Reich et al. (2008), CP = biogeomorphologische Sukzessionsphase nach Corenblit et al. (2007). Die Umweltfaktoren (schwarze Schrift) zeigen statistisch signifikante Zusammenhänge (verändert nach Zittel 2020).

Section 4, also animal-dispersal and self-dispersal. Burr dispersal was highest in the restored Section 4, whereas seed mass and wood density were highest in the regulated Section 3. Especially Sections 2–4 showed typical Ellenberg values like moisture value and nitrogen value and atypical traits like leaf endurance and life form (s. Fig. 5, part I). Looking at trait diversity the plots of the regulated Section 3 were similar and were organized in a close way to each other in the NMDS (Fig. 6). Unlike this, the trait diversity in the near-natural Section 2 and restored Section 4 was higher, focussing on the differences of the plots and the organization with high distances to each other.

Relationship between traits and habitat parameters

Looking at the NMDS ordination of traits in the space (Fig. 7) there were different relationships to habitat parameters. Seed mass, individual height and the Ellenberg values except of the light and continental values were correlated with increasing soil depth, increasing distance to the mean water and an advanced succession phase.

Plant traits like mean leaf length, water dispersal, wind dispersal, amount of woody plants, wood density, and the Ellenberg values for light and continentality were highly related to increasing indicators of high river dynamics like coverage of bare soil, morphodynamics and flood dynamics, wood damage, coverage of sand and gravel and more open canopy.

Discussion

A mosaic of different succession phases is typical for braided river ecosystems (Egger et al. 2007; Egger et al. 2022) which was also represented by different traits occurring side by side in the four study sections at the Upper Isar. Trait diversity of the overgrown diverted reach within Section 1 decreased due to the lack of bedload and the resulting lower intensity of disturbance (Fig. 5). The trait characteristics were still very similar to those of the near-natural system in Section 2. However, the cover of woody plants (especially willow shrubs) increased in this reach in the last decades and the species composition and traits might change on a long term (Reich et al. 2008; Juszczyk et al. 2020).

Section 2 is only affected by water diversion; it is used as a near-natural reference for North alpine braided rivers (Juszczyk et al. 2020). Plants need to be adapted to the frequent disturbances which is expressed by their traits (Parkhurst & Loucks 1972). The traits in Section 2 were characterised by a short leaf length and a low seed mass (Fig. 5). Besides, early pioneer phases were still present which causes according to Fukami et al. (2005) a higher trait diversity, i.e. a higher dispersion in the NMDS (Fig. 6). This high dispersion of the near-natural Section 2 showed the high trait dissimilarity of this section compared to the restored Section 4. In the regulated Section 3, on the other hand, the plots were similar in the expression of the traits, which resulted in an orientation of the plots close to each other (Fig. 6).

Compared to the traits of the near-natural Section 2, the traits of Section 3 were characterised by high seed mass, high wood density and generally low trait diversity (Fig. 5). A correlation could be observed here due to the change in disturbance intensity caused by retention of flood peaks and bedload in the Sylvenstein reservoir as well as bank protection, which allows no relocation. Thus, there is an adaptation to these more stable conditions with progressive succession. Besides, it was striking here that the plots within Section 3 could almost exclusively be classified in the biogeomorphological and the ecological phase of the fluvial biogeomorphic succession concept of Corenblit et al. (2007). Considering that there are no pioneer communities in Section 3 it seems reasonable that the trait diversity is lower here (Fukami et al. 2005). In terms of traits, the regulated Section 3 could be assessed as completely altered and impaired.

In contrast, the trait values in the plots of the restored Section 4 had a wide range of variation. However, the traits did not correspond to the near-natural Section 2 (Fig. 5, Fig. 6). Trait diversity was high, which can be attributed to the newly created pioneer sites (Fukami et al. 2005). However, a full adaptation of the vegetation to the conditions prevailing in the natural system takes time (Bartha et al. 2003; Diggelen et al. 2001; Prach et al. 1999). Thus, it takes more than 20 years after restoration for the complete reestablishment of species (Bayerisches Landesamt für Umwelt 2011). Although the habitat parameters were like those of near-natural diverted Section 2 and the trait diversity was also similar (Fig. 6), the typical species were different (Fig. 5). Colonisation with the typical species occurring in the natural system can only take place via water- and wind dispersal. However, the area can again be assessed as only moderately impacted.

Résumé

The four river sections along the Upper Isar are characterised by different habitat parameters and plant species. The overgrown diverted Section 1 with impacts on the hydro- and morphodynamic regime is characterised by a high proportion of woodland. The expression of the species here is shifted to the dryness-adapted range. However, the habitat parameters and traits here are most like the near-natural Section 2. Besides, the latter is also characterised by high diversity of species and traits.

The removal of morpho- and hydrodynamics in the regulated Section 3 leads to drastic changes in the river and riparian ecosystem. This leads to high amounts of advanced phases of succession resulting in similar individual sites in terms of their species and trait composition.

In the restored Section 4, removing of the bank protection and adding of bedload by side erosion were planned to re-initiate the characteristics of the former braided river. This leads to an approximation to the near-natural Section 2 regarding the habitat parameters and clear differences to the regulated Section 3. The trait diversity is increasing again and is similar to that of Section 2. Trait characteristics, however, are still different to the near-natural diverted Section 2.

Our results indicate that traits thus enable a superordinate view of human interventions on rivers. Natural sites can be investigated as trait references and can be used as indicators of the deviating states of restored river reaches in terms of their expression and diversity. The consideration of traits is also advantageous in the global comparison of restored rivers. As different species occur in different climatic regions, they still had to adapt to the similar site conditions with frequent disturbances and stresses of braided rivers and probably developed corresponding traits. The comparison of traits could therefore be a valuable tool and should be tested on other rivers.

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Literature

Bartha S, Meiners S J, Pickett S T A, Cadenasso M L (2003) Plant colonization windows in a mesic old field succession. Applied Vegetation Science 6, 205–212. DOI: https://doi.org/10.1111/j.1654-109X.2003.tb00581.x

Bayerisches Landesamt für Umwelt (2011) Flusslandschaft Isar im Wandel der Zeit. LfU, Augsburg, 104p.

BayernAtlas [WWW Document] (2019) Bayernatlas.de. URL http://www.bayernatlas.de (accessed 28-11-2022)

Catford J, Jansson R (2014) Drowned, buried and carried away: Effects of plant traits on the distribution of native and alien species in riparian ecosystems. New Phytologist 204, 19–36. DOI: https://doi.org/10.1111/nph.12951

Corenblit D, Baas A, Balke T, Bouma T, Fromard F, Garófano-Gómez V, González E, Gurnell A M, Hortobágyi B, Julien F, Kim D, Lambs L, Stallins J A, Steiger J, Tabacchi E, Walcker R (2015) Engineer pioneer plants respond to and affect geomorphic constraints similarly along water–terrestrial interfaces world-wide. *Global Ecology* and *Biogeography* 24, 1363–1376. DOI: https://doi.org/10.1111/geb.12373

Corenblit D, Steiger J, Gurnell A M, Naiman R J (2009) Plants intertwine fluvial landform dynamics with ecological succession and natural selection: a niche construction perspective for riparian systems. *Global Ecology* and *Biogeography* 18, 507–520. DOI: https://doi.org/10.1111/j.1466-8238.2009.00461.x

Corenblit D, Tabacchi E, Steiger J, Gurnell A M (2007) Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: A review of complementary approaches. Earth Science Reviews 84, 56–86. DOI: https://doi.org/10.1016/j.earscirev.2007.05.004

Diggelen R V, Grootjans A P, Harris J A (2001) Ecological restoration: State of the art or state of the science? Restoration Ecology 9, 115–118. DOI: https://doi.org/10.1046/j.1526-100x.2001.009002115.x

Egger G, Aigner S, Angermann K (2007) Vegetationsdynamik einer alpinen Wildflusslandschaft und Auswirkungen von Renaturierungsmaßnahmen auf das Störungsregime, dargestellt am Beispiel des Tiroler Lechs. Jahrbuch des Vereins zum Schutz der Bergwelt 72, 5–54

Egger G, Rood S B, Becker I, Betz F, Chepinoga V, Deil U, Lashchinskiy N, Magnusson B, Roth A, Stewart G, Troeva E, Müller N (2022) Riparian vegetation of gravel-bed rivers - a global review. Encyclopedia of Inland Waters. 2nd edition, Vol. 3, 182–213. DOI: https://doi.org/10.1016/B978-0-12-819166-8.00173-0

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. 6th ed., UTB-Verlag, Stuttgart, 1334p. ISBN: 9783825281045

Fischer M A, Oswald K, Adler W (2008) Exkursionsflora für Österreich, Liechtenstein und Südtirol. 3. Auflage. 1391p. ISBN: 978-3-85474-187-9

Fukami T, Bezemer T M, Mortimer S R, van der Putten W H (2005) Species divergence and trait convergence in experimental plant community assembly. Ecology Letters 8, 1283–1290. DOI: https://doi.org/10.1111/j.1461-0248.2005.00829.x

Hauer F R, Locke H, Dreitz V J, Hebblewhite M, Lowe W H, Muhlfeld C C, Nelson C R, Proctor M F, Rood S B (2016) Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes. Science Advances 2, e1600026. DOI: 10.1126/sciadv.1600026

Hettrich R, Ruff A (2011) Freiheit für das wilde Wasser - Die WWF-Alpenflussstudie. WWF Deutschland, 140p.

Hohensinner S, Besci R, Egger G, Fiebig M, Knopper F, Muhar S, Piégay H, Polt R (2019) Morphology. The many faces of Alpine Rivers. In: Muhar S, Muhar M, Egger G, Siegrist D (Eds.): Rivers of the Alps. Diversity in Nature and Culture. Haupt-Verlag, Bern, 86–113. ISBN: 978-3-258-08114-4

Hohensinner S, Egger G, Muhar S, Vaudor L, Piégay H (2021) What remains today of pre-industrial Alpine rivers? Census of historical and current channel patterns in the Alps. River Research and Applications 37, 128–149. DOI: https://doi.org/10.1002/rra.3751

Juszczyk I, Egger G, Müller N, Reich M (2020) Auswirkungen der Ausleitung der Oberen Isar auf die Auenvegetation. Auenmagazin 17, 28–37

Keddy P A (1992) Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3, 157–164. DOI: https://doi.org/10.2307/3235676

Maier F, Becker I, Speer F, Egger G (2021) Die Obere Isar – eine verlorene Wildflusslandschaft? Eingriffe und deren Auswirkungen sowie Renaturierungspotenziale der Oberen Isar vom Krüner Wehr bis Bad Tölz. Jahrbuch des Vereins zum Schutz der Bergwelt 86, 3–38

McIntyre S, Lavorel S, Landsberg J, Forbes T D A (1999) Disturbance response in vegetation – towards a global perspective on functional traits. Journal of Vegetation Science 10, 621–630. DOI: https://doi.org/10.2307/3237077

Muhar S, Arnaud F, Aschwanden H, Binder W, Broggi M, Greimel F, Knopper F, Michor K, Morandi B, Piégay H (2019) Restoration. New life for the rivers of the Alps. In: Muhar S, Muhar A, Egger G, Siegrist D (Eds.) Rivers of the Alps. Diversity in Nature and Culture. Haupt-Verlag, Bern, 320–343

Müller N (1991) Veränderungen alpiner Wildflußlandschaften in Mitteleuropa unter dem Einfluß des Menschen. Augsburger Ökologische Schriften 2, 9–30

Müller N (1995 a) Wandel von Flora und Vegetation nordalpiner Wildflusslandschaften unter dem Einfluß des Menschen. Berichte Bayer. Akademie für Naturschutz Landschaftspflege 19, 125–187

Müller N (1995 b) River dynamics and floodplain vegetation and their alterations due to human impact. Archiv für Hydrobiologie, Large Rivers 9, 477–512. DOI: https://doi.org/10.1127/lr/9/1996/477

Parkhurst D F, Loucks O L (1972) Optimal leaf size in relation to environment. Journal of Ecology 60, 505–537. DOI: https://doi.org/10.2307/2258359

Patten B C, Auble G T (1981) System theory of the ecological niche. The American Naturalist 117, 893–922. DOI: https://doi.org/10.1086/283777

Poschlod P (2016) Die Obere Isar – Flusslandschaft im Wandel: Eine „Kulturgeschichte“ wasserbaulicher Maßnahmen und der Waldweide. Tuexenia Beihefte 9, 85–105

Prach K, Pyšek P, Šmilauer P (1999) Prediction of vegetation succession in human-disturbed habitats using an expert system. Restoration Ecology 7, 15–23. DOI: https://doi.org/10.1046/j.1526-100X.1999.07102.x

Reich M, Bargiel D, Rühmkorf H (2008) Die Obere Isar zwischen Fkm 253 und Fkm 232: Veränderungen der Vegetationsverhältnisse zwischen 1958 und 2006, Auswirkungen der Hochwasser 1999 und 2005 und Situation und Perspektive ausgewählter Zielarten. Gutachten im Auftrag des Bayerischen Landesamtes für Umwelt und des Wasserwirtschaftsamtes Weilheim (Schlussbericht). Hannover, 20p.

Reich M, Rethschulte C (2021) Beachlife an der Oberen Isar: räumliche und zeitliche Dynamik in einem Hotspot der Biodiversität. Gutachten im Auftrag des Bayerischen Landesamts für Umwelt, 70p.

Richardson S J, Williams P A, Mason N W H, Buxton R P, Courtney S P, Rance B D, Clarkson B R, Hoare R J B, John M G S, Wiser S K (2012) Rare species drive local trait diversity in two geographically disjunct examples of a naturally rare alpine ecosystem in New Zealand. Journal of Vegetation Science 23, 626–639. DOI: https://doi.org/10.1111/j.1654-1103.2012.01396.x

Roeder M, Hölscher D, Kossmann-Ferraz I D (2012) Traits and growth of liana regeneration in primary and secondary forests of Central Amazonia. Applied Vegetation Science 15, 108–118. DOI: https://doi.org/10.1111/j.1654-109X.2011.01152.x

Schauer T (1998) Die Vegetationsverhältnisse an der Oberen Isar vor und nach der Teilrückleitung. Jahrbuch des Vereins zum Schutz der Bergwelt 53, 131–183

Speer F (1977) Das Problemgebiet Obere Isar - Entwicklung - Zustand- Lösungsvorschläge. Dargestellt am Beispiel der Isarauen zwischen Lenggries und Bad-Tölz. Diploma Thesis at the University of Munich-Weihenstephan, 193p.

Tockner K, Stanford J A (2002) Riverine flood plains: present state and future trends. Environmental Conservation 29, 308–330. DOI: 10.1017/S037689290200022X

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116, 882–892. DOI: https://doi.org/10.1111/j.0030-1299.2007.15559.x

WWF Deutschland (2022): Mehr Power für die Isar. WWF Deutschland, 22p.

Zittel A (2020) Funktionale Traits als Indikatoren für die Beurteilung von Eingriffen an Umlagerungsflüssen – am Beispiel der Oberen Isar. Master thesis at the Karlsruhe Institute of Technology (KIT), 90p. + Appendix

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