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The overlooked contribution of a fish bypass channel to the density and diversity of macroinvertebrate drift in a heavily modified river system

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Abstract

The freshwater biodiversity decline affects all trophic levels, prompting restoration efforts. While habitat restoration for fish is well-studied, habitat restoration to benefit other sensitive taxa such as Ephemeroptera, Plecoptera, and Trichoptera (EPT) remains poor. Consequently, this study investigated the habitat function of a man-made nature-like bypass system for EPT taxa in a highly modified alpine river with several drift feeding fishes. Spatially and temporally distributed drift samples were used to test the hypotheses that the bypass (a) enhances the density of drifting individuals compared to the main river and (b) diversifies drift assemblages compared to the main river. Mean drift density of EPT taxa was lowest in the main stem of the river close to the inlet of the bypass (38.24 Ind./$100m^3$) and significantly increased toward the downstream direction of the bypass, near the outflow (61.49 Ind./$100m^3$). In addition, drift assemblages significantly changed from the main stem to the bypass and the number of EPT taxa detected more than doubled (main stem: 16 genera; last site in the bypass: 33 genera), indicating that the bypass can provide a macroinvertebrate source to the main stem. Seasonal and diel drift patterns were similar to those observed in natural streams, underpinning the finding that nature-like bypass systems can feature an EPT community similar to natural rivers. This study aligns with a growing body of evidence on the habitat function of nature-like bypass systems for aquatic taxa and highlights the importance of this restoration measure beyond the aspect of solely restoring habitat connectivity.

KEYWORDS
freshwater biodiversity conservation, hydropower mitigation, river restoration, semi-aquatic insects, spatio-temporal drift pattern

1 | INTRODUCTION

The tangible decline of freshwater biodiversity in recent decades is largely attributed to the anthropogenic alteration of rivers, which has led to a widespread loss of quantity, quality, and connectivity of aquatic habitats (Stendera et al., 2012; Tickner et al., 2020). Consequently, many

aquatic biota substantially declined in abundance and distribution range, or have already become extinct (IUCN, 2021). According to the Living Planet Index, all taxonomic groups are exposed to higher risk of extinction in freshwater ecosystems compared to the terrestrial ecosystems, with almost one of three species being threatened with extinction (Almond, Grooten, & Peterson, 2020). Since 1970, freshwater

populations have declined on average by 84% (Almond et al., 2020). Traditionally, conservation of freshwater biodiversity has focused on prominent species such as the fauna of mega-fish (Albert et al., 2021; He et al., 2019). On the other hand, declines of less charismatic groups such as insects have only recently received attention (Jähnig et al., 2021), yet must be considered in integrative concepts of freshwater biodiversity conservation (Geist, 2011). This development has prompted many restoration efforts in the past decades, which aim to improve the quality and connectivity of habitats in riverine ecosystems (Geist & Hawkins, 2016; Jungwirth, Muhar, & Schmutz, 2002; Ormerod, 2004; Wohl, Lane, & Wilcox, 2015). A key aspect in river restoration is the reestablishment of longitudinal migration routes for aquatic biota, particularly fish, which can be achieved by removing migration barriers such as dams (Sneddon, Barraud, & Germaine, 2017). Since this is a difficult task in most places, connectivity is much more often restored through the construction of bypass facilities. These systems can range from rather technical solutions such as fish lifts or pool passes made of concrete to nature-like construction schemes (Larinier & Marmulla, 2004). While rather technical solutions primarily target the migratory function, nature-like fish bypass channels mimic habitats of formerly free-flowing river stretches by including habitats of high and low current as well as variable bed material (Meulenbroek, Drexler, Nagel, Geistler, & Waidbacher, 2018; Pander, Mueller, & Geist, 2013; Pander, Nagel, & Geist, 2021). In recent years, an increasing number of studies have demonstrated that these types of fish passes provide important habitats for spawning and foraging, especially for threatened fish species (Meulenbroek et al., 2018; Nagel et al., 2021; Pander et al., 2013; Tamario, Degerman, Donadi, Spjut, & Sandin, 2018) and in situations where they increase temperature and flow diversity (Pander, Nagel, & Geist, 2021).

River restoration measures and their assessment primarily target fish species, while the response of other biota, for example, aquatic insect communities, remains poorly understood. In a comprehensive review, Ormerod (2004) revealed that macroinvertebrates are included in river restoration studies only half as often as fish. Although aquatic biodiversity losses have specifically been documented in upper trophic levels (e.g., mammals and fishes; Petchey et al., 2004), they are evident in all taxonomic groups and also occur in lower trophic levels such as phytoplankton (Urrutia-Cordero et al., 2017) and the macroinvertebrates, an enormously diverse group (Su et al., 2021). There is a long list of critically endangered freshwater invertebrates comprising species such as the freshwater pearl mussel (Bauer, 1988; Geist, 2010), crayfishes (Richman et al., 2015), and aquatic insects, among which EPT taxa (mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera)) are particularly affected (Bojková, Rádková, Soldán, & Zahrádková, 2014; DeWalt, Favret, & Webb, 2005; Jähnig et al., 2021; Pond, 2010; Pond, 2012). Aquatic insects play an important role in the food web of riverine ecosystems, both as a bottom-up food source for fish and amphibians as well as a top-down processor of energy and nutrients (Suter & Cormier, 2015; Wallace & Webster, 1996). This holds especially true in rivers like the Inn where several fish species such as grayling (*Thymallus thymallus* L.) and brown trout (*Salmo trutta fario* L.) are typical drift feeders that heavily feed on such species. Aquatic insects are also indicators for the chemical and structural quality of a river stretch and therefore constitute important assessment criteria in river monitoring programs such as the European Water Framework Directive (WFD; Council of the European Communities, 2000). Similar to fish, macroinvertebrates are fast colonizers of new aquatic habitats (Mackay, 1992; Pander, Mueller, Sacher, & Geist, 2016). Whilst most insects have adult flying stages facilitating their movement over dams and weirs, such structures can act as important barriers for the movement of less mobile taxa such as molluscs, crustacean, and paurometabolous insects. In such cases, fish passes can provide important corridors for upstream movements as it has been documented for gammarids (Rawer-Jost, Kappus, Böhmer, Jansen, & Rahmann, 1998). Gustafsson, Österling, Skurdal, Schneider, and Calles (2013) provided early evidence that a high degree of habitat heterogeneity in nature-like constructed fish passes facilitates the colonization by macroinvertebrates from the main river. However, the role of nature-like fish passes as a biodiversity, abundance, and food source for the main river is not yet understood, but may be of particular importance in heavily modified waterbodies, where these types of bypass facilities provide a high degree of habitat quality compared to the main river.

This study evaluated the function of a nature-like bypass system as a drift corridor and diversity source for macroinvertebrates, specifically EPT taxa, by using a comparison of drift samples from sites distributed along a downstream gradient. We hypothesized that the constructed nature-like bypass provides habitat for EPT taxa and consequently (a) enhances the density of drifting macroinvertebrates compared to the main river, and (b) diversifies drift assemblages compared to the main river.

2 | MATERIAL AND METHODS

2.1 | Study area

This study was conducted at the large alpine River Inn. Like many other (pre-) alpine rivers (for reference see Tockner et al., 2003; Ward et al., 1999) this river was formerly characterized by a braided anabranching river course, comprising a rich habitat mosaic of the main stem and several side branches as well as manifold floodplain habitats with differing degrees of connectivity. The fish community of this river was formerly dominated by drift feeding salmonids such as grayling and brown trout as well as several rheophilic cyprinid species. To date these species still exist, but the community has shifted toward less specialized and ubiquitous species (Pander, Nagel, & Geist, 2021; Pander, Nagel, Ingermann, & Geist, 2021). Anthropogenic alteration, particularly bank stabilization and hydropower installation, changed the former river course dramatically to a widely dammed and uniform waterbody (Pander, Nagel, & Geist, 2021). Despite these morphological alterations, the hydrograph of this river fluctuates widely, mainly driven by snow- and glacier melt. This leads to high turbidity and relatively cold water temperatures during spring and summer (Pander, Nagel, Ingermann, & Geist, 2021). Currently, the catchment of the River Inn is the subject of a large restoration program which targets
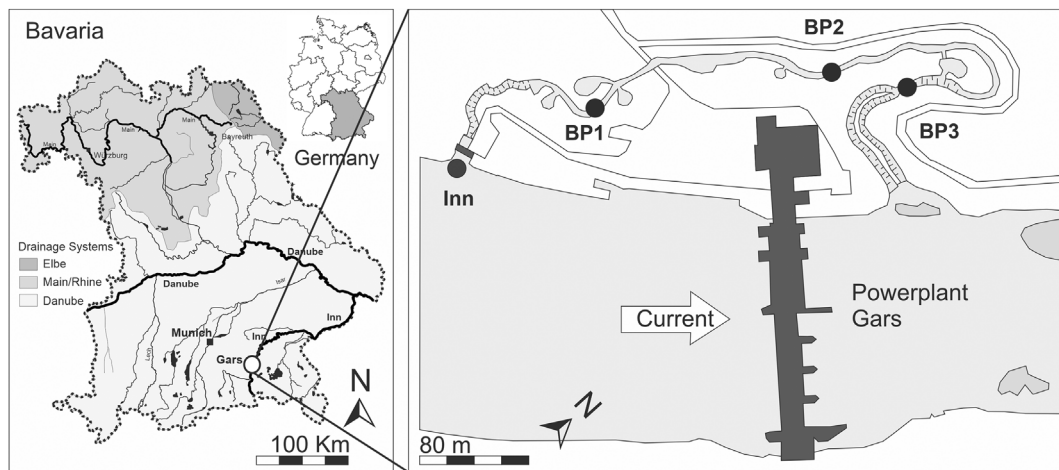
FIGURE 1 Map of the study area (left) and positioning of sampling sites (right)

the quality and connectivity of fish habitats. To restore longitudinal connectivity, bypass systems at hydropower facilities are implemented. Whenever financial and spatial constraints allow, these are constructed in a nature-like way, with the intention to resemble side-branches of the former braided river course.

As many weirs of the River Inn are already equipped with nature-like bypass channels, this study focused on a representative model bypass system at the hydropower station Gars am Inn (48°15' N; 12°31' E) as the study site (Figure 1). The bypass has a length of 650 m and is fed with a constant flow of ~900 ls^{-1} by a concrete underflow weir, which supplies water from the River Inn. At the entrance and at the exit, the bypass is constructed with engineered elements (pool pass). In between, it follows a nature-like construction scheme, comprising gravelly substrate, a high variability in water depths, flow velocities and structures such as dead wood and current deflectors made of boulders, which are intended to provide additional aquatic habitats.

2.2 | Study design

2.2.1 | Spatial patterns

To assess the spatial drift patterns of macroinvertebrates, drift was investigated in the main stem of the River Inn, at 2 m distance above the inlet to the bypass system and at three additional sites located further downstream in the bypass. Each site had a minimum distance of 150 m to the next site. No additional sites in the main stem were sampled, as this study explicitly aimed to assess spatial variation of macroinvertebrate drift from the inflow to the outflow of the bypass. The drift nets used consisted of rectangular aluminum frames for the mouth and tear-resistant polyester (155 meshes cm^{-2}) for the nets (Nagel et al., 2021). For representative sampling, sites were evenly distributed along the course of the bypass, with similar water depths (Table 1). The whole water column was sampled at each site by using two nets stacked over each other, resulting in eight nets used per sampling interval.

2.2.2 | Seasonal and diel patterns

To investigate seasonal patterns in the drift of macroinvertebrates, drift was studied for a total of 6 days over a period of 11 weeks (April 20–June 28) with samples taken every 8–14 days. At each day of sampling, nets were first set at 10 a.m. To also account for diel patterns, sampling was subsequently repeated every ~4 hr until ~6 a.m. the following day. This protocol covered periods of day, dusk, night and dawn and resulted in 288 samples in total. The changing times of dusk at dawn during the period of investigation were accounted for by adjusting these times of sampling accordingly. Nets were set for 30 min each time of sampling resulting in 3 hr of sampling time per 24 hr.

2.2.3 | Sample processing and taxonomic identification

Samples were directly checked for invertebrates in a field lab. Invertebrates were separated from drifting debris and preserved in ethanol (96%). Subsequently, samples were brought to the laboratory and specimens were determined at a first step to order level. Second, the orders EPT were further identified to genus level using established taxonomic keys (Families: Lechthaler, 2009; Trichoptera: Lechthaler & Stockinger, 2005; Ephemeroptera: Bauernfeind & Lechthaler, 2014; Plecoptera: Schmedtje, Kohmann, & Burmeister, 1992). All specimens were counted and identified under a stereoscope Olympus SZX10 (Olympus Deutschland GmbH).

2.2.4 | Abiotic variables

To calculate densities of drifting invertebrates, flow velocity was determined at six measuring points in the net opening using an electromagnetic water flow meter (Ott MF pro, Ott HydroMet GmbH, Kempten, Germany) following the approach described in Nagel et al.

TABLE 1 Abiotic variables measured during the period of investigation; values are given as means ± standard deviation. T = Temperature, O_2 = oxygen concentration, EC = electric conductance (related to 20°C)

	Flow velocity (ms^{-1})	Depth (m)	T (°C)	O_2 (mg/L)	EC (µS cm^{-1})	pH	Turbidity (NTU)
River Inn	0.12 ± 0.02	0.64 ± 0.06	12.6 ± 2.8	10.8 ± 0.9	274 ± 70	7.2 ± 0.3	52.6 ± 46.7
BP1	0.69 ± 0.10	0.58 ± 0.02	12.6 ± 2.8	10.7 ± 0.9	274 ± 70	7.2 ± 0.2	51.6 ± 47.2
BP2	0.56 ± 0.06	0.57 ± 0.02	12.7 ± 2.8	10.8 ± 0.9	274 ± 71	7.1 ± 0.2	48.5 ± 45.0
BP3	0.62 ± 0.08	0.60 ± 0.02	12.8 ± 2.9	10.8 ± 0.9	274 ± 70	7.1 ± 0.2	47.4 ± 41.9

(2021). To further characterize abiotic conditions during the period of investigation, a hand-held Multi 3,430 device (WTW GmbH, Weilheim, Germany) was used to measure dissolved O_2 (mg/L), water temperature (°C), electric conductance (µS/cm, related to 20°C), and pH at each site. Turbidity (nephelometric turbidity unit, NTU) was measured accordingly with three 20 ml subsamples taken from running water at each site using a PhotoFlex Turb handheld field measurement unit (WTW GmbH, Weilheim, Germany). All measurements were carried out once at each sampling day between 3 and 5 p.m.

2.2.5 | Data analysis

To standardize catch data, drift densities (x) given as number of invertebrates per 100 m^3 of filtered water were determined separately for each net. First, filtered water volume for each sample was calculated by multiplying the average flow velocity (v) by the exposure time (1,800s) and the net opening area (0.072 m^2). Subsequently, caught individuals from each sample (n) were divided by the filtered water volume and finally multiplied by 100. Throughout all samples, sampled water volume ranged from 11.8 to 107.2 m^3 (mean = 65.7 m^3).

$$x = \left(\frac{n}{v\frac{m}{s} * 1,800s * 0.072\,m^2} \right) * 100$$

Shapiro–Wilk and Levene tests were applied to check for normal distribution and homogeneity of variances in the spatial comparison of drift densities and taxa richness. Since the analyzed data did not follow normal distribution or homogeneity of variances, differences in drift densities and taxa richness between the investigated sites were tested with Kruskal–Wallis tests and post hoc Mann–Whitney U tests using standard R (version 4.1.2, R Core Team, 2019). Distribution of spatial drift densities and taxa richness were visualized in box plots using the package ggplot 2 (version 3.3.5, Wickham, 2016) in R. To analyze spatial and temporal changes in the drifting invertebrate assemblages, Bray-Curtis-similarities from taxa abundance data were computed in PRIMERv7 (Clarke, Gorley, Somerfield, & Warwick, 2014). Based on the calculated Bray-Curtis resemblance matrix an analysis of similarities (ANOSIM) was applied to test for significant differences in the taxa composition among sampling sites (spatial), months (seasonal) and daylight conditions (diel). Spatial differences in drifting EPT assemblages were visualized by metric multidimensional scaling of 75 bootstrap averages for each group based on the same

Bray-Curtis-similarities. Differences in the spatial distribution among the investigated sites were analyzed in greater detail for each of the four most abundant Ephemeroptera genera (*Baetis* Leach, 1815, *Ecdyonurus* Eaton, 1868, *Heptagenia* Walsh, 1863, *Serratella* Edmunds, 1959), Plecoptera genera (*Isoperla* Banks, 1906, *Leuctra* Stephens, 1836, *Protonemura* Kempny, 1898, *Amphinemura* Ris, 1902), and Trichoptera genera (*Hydropsyche* Pictet, 1834, *Rhyacophila* Pictet, 1834, *Psychomyia* Latreille, 1829, *Hydroptila* Dalman, 1819) by comparing individual drift densities in horizontal barplots. The same taxa were used for visualizations of the seasonal and diel turnover. Taxa-specific distribution over the period of investigation was visualized in estimated kernel density curves using the packages ggplot2 (version 3.3.5, Wickham, 2016) and plotly (version 4.10.0, Sievert, 2020) and the function "stat_density_ridges" from the package ggridges (version 0.5.3, Wilke, 2018) in R (version 4.1.2, R Core Team, 2019). Diel patterns were assessed by calculating mean abundances (± SD) for each sampling time and visualized using scatterplots with error bars. Significance was accepted at $p < .05$ for all statistical analyses.

3 | RESULTS

During a period of 11 weeks and 288 drift samples taken, 20,925 drifting macroinvertebrates were caught. Drift included EPT taxa (47.66%) and the orders Diptera (35.12%), Oligochaeta (11.70%), Amphipoda (2.86%), and Coleoptera (1.51%). All other orders were represented in shares <1% (Table S1). Considering EPT taxa only, Ephemeroptera (61.36%) was the most abundant order, followed by Trichoptera (21.77%) and Plecoptera (16.88%). At the genus level, *Baetis* (Ephemeroptera; 45.75%) was the most abundant taxon followed by *Isoperla* (Plecoptera; 14.85%) and *Hydropsyche* (Trichoptera; 13.15%; Table 2).

3.1 | Spatial patterns

Mean drift density of EPT taxa was lowest in the main stem River Inn (38.24 Ind./100m^3 ± 21.33) and increased to the first site in the bypass BP1 (51.42 Ind./100m^3 ± 29.51), yet this difference was not significant (Figure 2). Drift densities in the more downstream located sites in the bypass BP2 (48.23 Ind./100m^3 ± 37.46) and BP3 (61.49 Ind./100m^3 ± 42.70) were significantly higher compared to the River Inn (Figure 2).

| Order/genus	n	%	River Inn	BP1	BP2	BP3
Ephemeroptera	6,119	61.36	×	×	×	×
Baetis	4,563	45.75	×	×	×	×
Caenis	12	0.12	×		×	×
Ecdyonurus	1,090	10.93	×	×	×	×
Ephemera	7	0.07	×	×	×	×
Ephemerella	19	0.19		×	×	×
Habroleptoides	5	0.05		×	×	×
Heptagenia	283	2.84	×	×	×	×
Paraleptophlebia	10	0.10		×	×	×
Rhithrogena	41	0.41	×	×	×	×
Serratella	87	0.87	×	×	×	×
Torleya	2	0.02			×	×
Plecoptera	1,683	16.88	×	×	×	×
Amphinemura	29	0.29		×	×	×
Brachyptera	1	0.01				×
Chloroperla	1	0.01				×
Dinocras	8	0.08		×	×	×
Isoperla	1,481	14.85	×	×	×	×
Leuctra	107	1.07		×	×	×
Nemoura	20	0.20		×	×	×
Protonemura	36	0.36		×	×	×
Trichoptera	2,171	21.77	×	×	×	×
Allogamus	69	0.69	×	×	×	×
Brachycentrus	4	0.04		×	×	×
Chaetopteryx	1	0.01			×	
Hydropsyche	1,311	13.15	×	×	×	×
Hydroptila	88	0.88		×	×	×
Lepidostoma	1	0.01				×
Limnephilus	4	0.04			×	×
Melampophylax	1	0.01		×		
Micropterna	2	0.02			×	×
Plectrocnemia	3	0.03			×	×
Polycentropus	78	0.78	×	×	×	×
Potamophylax	1	0.01	×			
Psychomyia	128	1.28			×	×
Rhyacophila	480	4.81	×	×	×	×
TOTAL	9,973	100.00				

TABLE 2 Absolute (n) and relative (%) distribution of all Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa and spatial occurrence of taxa

A significant change of spatial taxa composition was observed between the investigated sites (ANOSIM: Global R = 0.37, p < .001; Figure 3). Drift of EPT taxa (16 documented genera) in the River Inn was mainly composed of the genera *Hydropsyche* (42.42%), *Isoperla* (35.99%) and *Baetis* (12.34%). The same taxa also dominated the drift at the most upstream site of the bypass (BP1) close to its upstream entrance (*Hydropsyche* = 24.94%, *Isoperla* = 24.81%, *Baetis* = 20.58%), although community composition of EPT changed significantly (ANOSIM: R = 0.34, p < .001; Table 3) compared to the River Inn. At the BP1 site, EPT taxa richness increased to 26, including 12 new taxa compared to the main stem of the River Inn (Table 2). These included three of the four most abundant Plecoptera genera (*Amphinemura*, *Leuctra*, and *Protonemura*) and two of the most abundant Trichoptera genera (*Hydroptila*, *Psychomia*; Figure 4). At the more downstream BP2 site in the bypass, a further increase in EPT taxa richness was found (31 documented genera) and taxa composition differed significantly compared to the BP1 site (ANOSIM: R = 0.30, p < .001) and even stronger compared to the River Inn (ANOSIM: R = 0.77, p < .001). Drifting EPT assemblages showed the highest taxa richness in the BP3 site (33 documented genera), however taxa composition
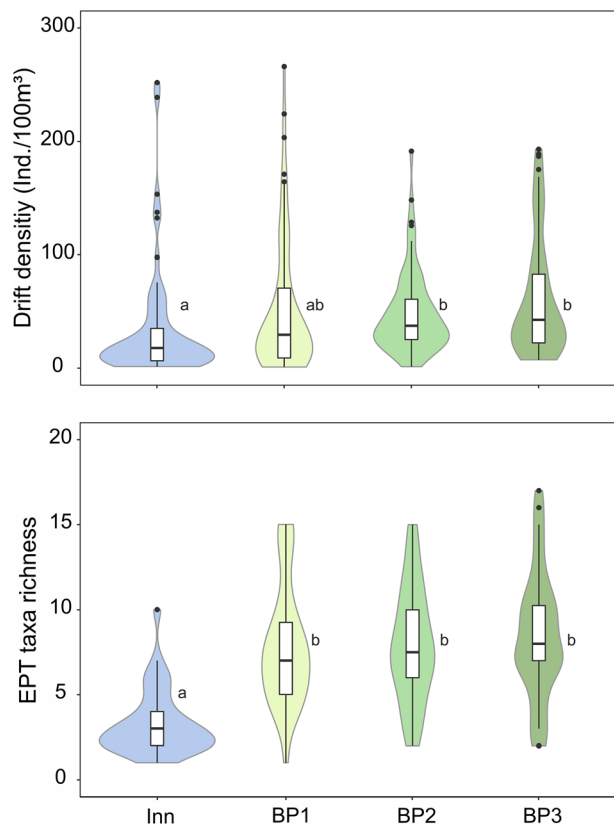
FIGURE 2 Spatial drift densities of all EPT taxa (upper panel) and spatial distribution of taxa richness of all EPT taxa (lower panel). Different small letters beside boxes represent significant differences. Note that the panel taxa richness represents absolute values [Color figure can be viewed at wileyonlinelibrary.com]
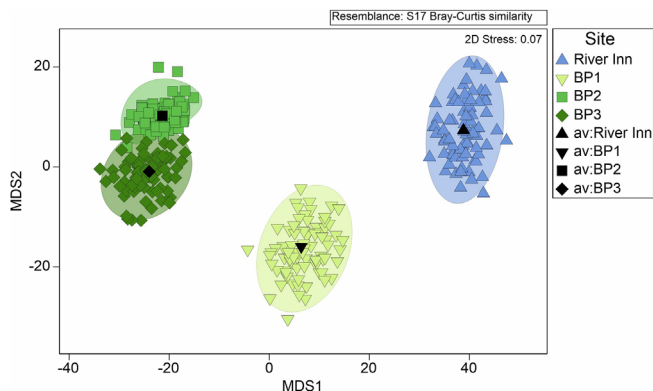
FIGURE 3 Metric multidimensional scaling (MDS) of bootstrap averages per site showing the spatial distribution patterns of the drifting EPT taxa assemblages based on drift densities. Bootstrap averages are based on pairwise Bray–Curtis similarities between each pair of sites calculated from the summed daily species composition. Shaded ellipses represent more than 95% of all bootstrap average points of each site, av: = average [Color figure can be viewed at wileyonlinelibrary.com]

was very similar compared to the BP2 site (ANOSIM: R = 0.01, p = .20; Figure 3). At these sites, drift was dominated by *Baetis* (BP2 = 61.62%, BP3 = 63.85%), followed by *Ecdyonurus*

TABLE 3 Results of ANOSIM testing for spatial, seasonal, and diel changes in the Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa composition.

|	Group comparison	R	p
Spatial	Inn–BP1	0.342	**<.001**
	Inn–BP2	0.767	**<.001**
	Inn–BP3	0.800	**<.001**
	BP1–BP2	0.302	**<.001**
	BP1–BP3	0.304	**<.001**
	BP2–BP3	0.013	.204
Seasonal	April–May	0.025	.050
	April–June	0.054	**<.05**
	May–June	0.011	.192
Diel	Day–Dusk	0.270	**<.01**
	Day–Night	0.233	**<.001**
	Day–Dawn	−0.003	.513
	Dusk–Night	−0.012	.628
	Dusk–Dawn	0.197	**<.001**
	Night–Dawn	0.201	**<.001**

Note: Significant differences of group comparisions are indicated in bold.

(BP2 = 11.40%, BP3 = 9.37%) and *Isoperla* (BP2 = 8.90%, BP3 = 8.87%; Figure 4). Taxa composition at the BP3 site differed significantly to the BP1 site (ANOSIM: R = 0.30, p < .001) and even stronger compared to the River Inn (ANOSIM: R = 0.80, p < .001).

3.2 | Seasonal and diel distribution

Weak changes were observed in the mean drift densities of EPT taxa between the months investigated (April = 55.18 Ind./100m^3, May = 42.86 Ind./100m^3, June = 53.78 Ind./100m^3), although the total number of detected EPT genera showed slightly greater differences (April = 27 genera, May = 19 genera, June = 21 genera). However, the seasonal distribution of EPT drift assemblages showed very weak variation (ANOSIM: Global R = 0.03; p < .05) and was significantly different only between April and June (ANOSIM: R = 0.05, p < .05; Table 3). The majority of the most common EPT taxa had their median of occurrence in April (n = 6), followed by May (n = 4) and June (n = 2; Figure 5). While several taxa showed strong peaks of occurrence in a short period of time (*Amphinemura*, *Leuctra*, *Protonemura*, *Hydroptila* in April/start of investigation period, and *Serratella* in June/end of investigation period), others (*Baetis*, *Heptagenia*, *Isoperla*, *Hydropsyche* and *Rhyacophila*) revealed a more continuous drift density during the whole study period (Figure 5).

For EPT taxa, a clear shift to nocturnal drift activity was evident, with highest mean drift abundance occurring at dusk (0.35 ± 0.06) followed by night sampling at 2 a.m. (0.30 ± 0.02). Drift distinctly decreased at dawn (0.12 ± 0.02) and was comparably low in all samples taken during daylight (10 a.m. = 0.09 ± 0.02; 2 a.m. = 0.08 ± 0.01; 6 p.m. = 0.07 ± 0.02). In addition, significant changes in the diel EPT taxa composition were
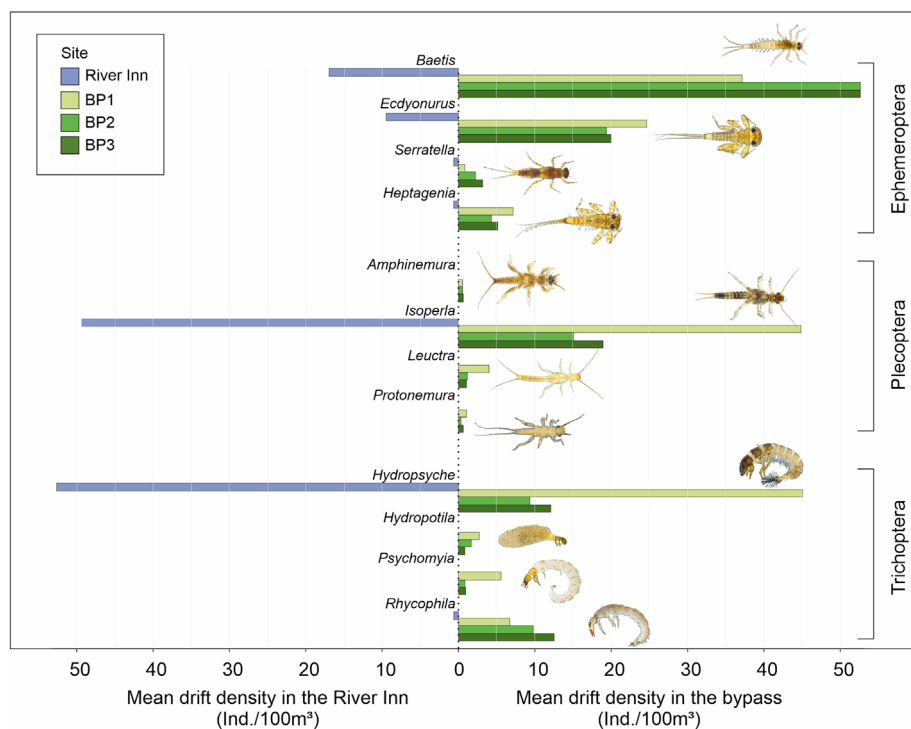
FIGURE 4 Genus-specific mean drift densities at the four investigated sites Inn, BP 1, BP 2, and BP 3. Bars to the left refer to drift densities in the main stem of the Inn, bars to the right to drift densities within the bypass. Note that five taxa, *Amphinemura* spec., *Leuctra* spec., *Protonemura* spec., *Hydroptila* spec., *Psychmoyia* spec. were exclusively found in the bypass [Color figure can be viewed at wileyonlinelibrary.com]

observed in relation to the time of day (ANOSIM: Global R = 0.15; $p < .001$). This was specifically evident when comparing drift assemblages of dusk and night with those of day and dawn (Table 3). Nocturnal drift prevailed in almost all examined taxa, except for the genus *Hydroptila*, which drifted in higher abundance during daylight (Figure 6). Moreover, *Rhyacophila*, *Baetis* and *Serratella* showed a diel distribution with less extreme diurnal-nocturnal variation in contrast to *Ecdyonurus*, *Heptagenia*, *Amphinemura*, *Isoperla* and *Leuctra*, which occurred almost exclusively during dusk or night sampling (Figure 6). Tendency for exclusive nocturnal drift activity appears to be common among all Plecoptera taxa, as well as for both genera of the Heptageniidae family (*Ecdyonurus* & *Heptagenia*).

4 | DISCUSSION

In light of a deepening biodiversity crisis in freshwaters, knowledge on the effectiveness of aquatic habitat restoration for all trophic levels is of crucial importance for future conservation efforts in these ecosystems. This study provides evidence that nature-like bypass channels comprise important habitats for EPT taxa as they increase drift densities and significantly diversify drift assemblages. These results are in line with previous findings on the habitat function of nature-like bypass channels for threatened fish species and highlight the importance of such restoration measures in heavily modified waterbodies beyond the aspect of restoring habitat connectivity.

4.1 | Spatial distribution

The results of this study clearly show that the output of aquatic insect larvae from the bypass into the River Inn distinctly exceeds the input

from the River Inn into the bypass, both in terms of density and diversity. The number of detected genera more than doubled from the main stem to the outflow of the bypass, thereby demonstrating that nature-like bypass channels can feature a rich EPT community. This finding is highlighted especially by Plecoptera taxa, where 8 of 10 detected genera were solely found drifting in the bypass. The distribution of aquatic insects in lotic ecosystems is mainly related to abiotic variables such as water temperature, bed material, water depth, and flow velocity (Faith & Norris, 1989; Pastuchová, Lehotský, & Grešková, 2008), as well as to biotic factors such as the presence of predators (Forrester, 1994) and the availability of food sources (Mackay, 1992). In terms of abiotic habitat conditions, shallow gravely riffles with high flows represent key habitats for many EPT taxa (Hansen & Closs, 2007). Concurrently these habitats are among the first to be lost during anthropogenic alteration of streams, particularly in alpine rivers (Woellner, Wagner, Crabot, & Kollmann, 2022). When adequately engineered, nature-like bypass waters can mimic these habitats (see also Gustafsson et al., 2013), which have previously been shown to also function as spawning grounds for several gravel spawning fish species with high conservation values (Meulenbroek et al., 2018; Nagel et al., 2021).

The high diversity of EPT taxa documented only 2 years after flooding of the bypass underlines previous findings that macroinvertebrates can be fast colonizers of aquatic ecosystems (Mackay, 1992; Pander et al., 2016). This also corresponds well to results from Gustafsson et al. (2013) who revealed that a nature-like fish bypass with similar dimensions was already colonized 2 years post-construction by 63% of the benthic fauna families found in the wild reference streams. Macroinvertebrates have different pathways to colonize new habitats. First, colonization can occur by adult insects that originate from nearby water bodies and lay their eggs in new habitats. However, this
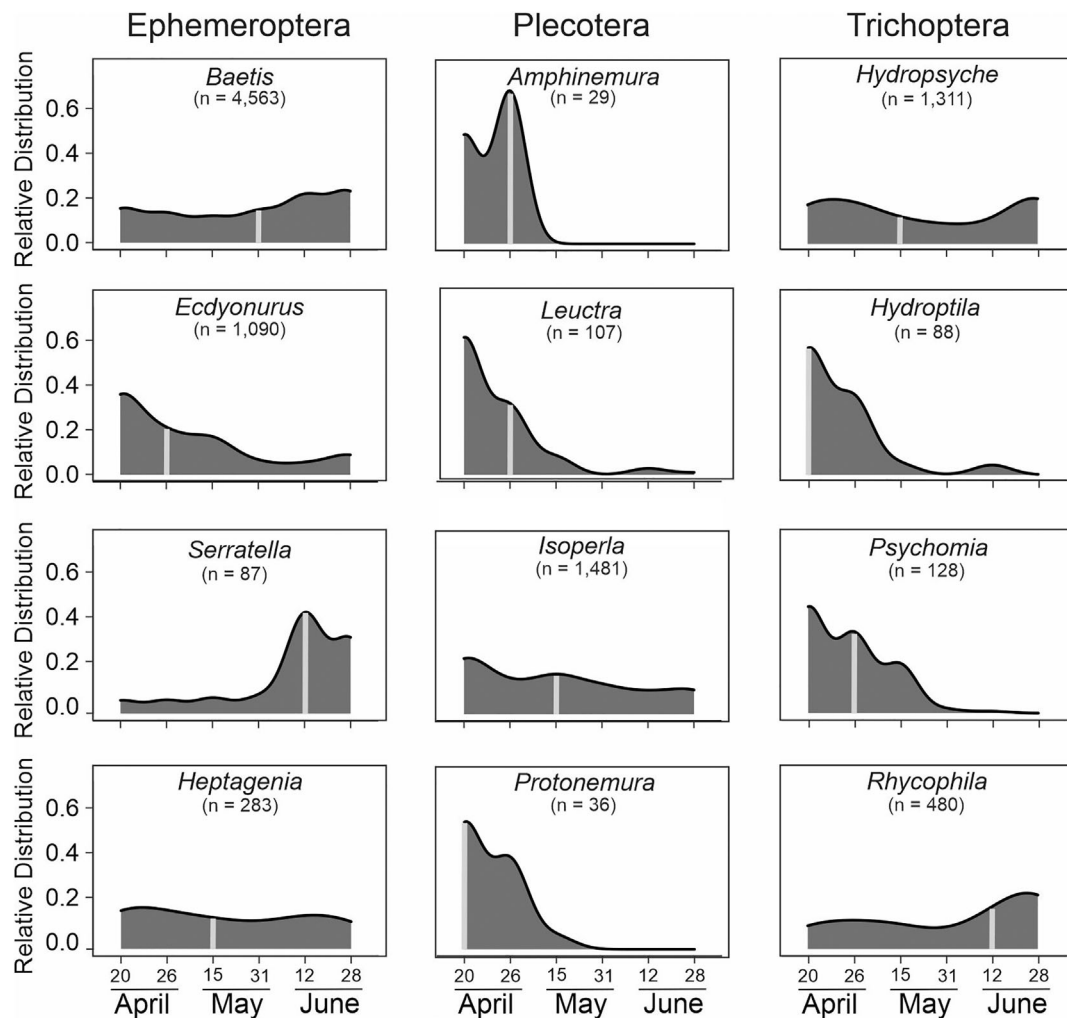
FIGURE 5 Density curves showing the estimated kernel density of drift for selected EPT taxa. Median is marked in light grey

scenario should be examined with caution for the stoneflies detected in our study, as this group can show a restricted mobility in the adult stage, which may prevent it from crossing even quite small barriers (Hynes, 1976; Malmqvist, 2000). Second, comparable to fish larvae (Lechner, Keckeis, & Humphries, 2016; Nagel et al., 2021), macroin-vertebrates are known to colonize new habitats via downstream directed drift processes from upstream regions (Mackay, 1992). Third, upstream directed movements, for example, through fish bypasses, have been documented for some taxa (Rawer-Jost et al., 1998).

It should be noted that our study design cannot completely rule out the input of single individuals of rare species from upstream sources other than the bypass, particularly since it does not provide a comprehensive picture of the occurrence of EPT taxa in the main stem (which would be difficult given the dimensions and flow of the River Inn). This must also be considered with regard to flow velocities and the related filtered water volume, which were distinctly lower at the influence of the bypass than in the sites located in the bypass itself. These differences in the water volume filtered by the drift nets at the inflow and the sites within the bypass may result in an underes-timation of the taxa richness for the main stem. The observed lower

densities at this site corrected by the water volume still strongly indi-cate that the lower diversity value is not driven by such sampling effects. Additionally, drift propensity can vary among taxa as detected by Rader (1997), which could be a reason that some potentially occur-ring taxa might have been missed with this sampling technique. How-ever, the significant increase in density and diversity of drifting EPT taxa in the course of the bypass clearly indicates that these systems can provide important compensatory habitats for the EPT-community and comprise a source function for biodiversity to the heavily modi-fied main river.

The high density and diversity of aquatic insect larvae can make an important contribution to the food web of nature-like bypass sys-tems, as previous studies have shown that these restoration measures in the River Inn are also used by highly endangered fish species such as the European grayling, which has suffered from severe declines throughout the area (Mueller, Pander, & Geist, 2018). Observations revealed that this species uses nature-like bypass systems as spawn-ing habitat in spring (Nagel et al., 2021), but also as foraging habitat throughout the year, as it was documented in the bypass in compara-tively high densities year-round (Pander, Nagel, & Geist, 2021). The
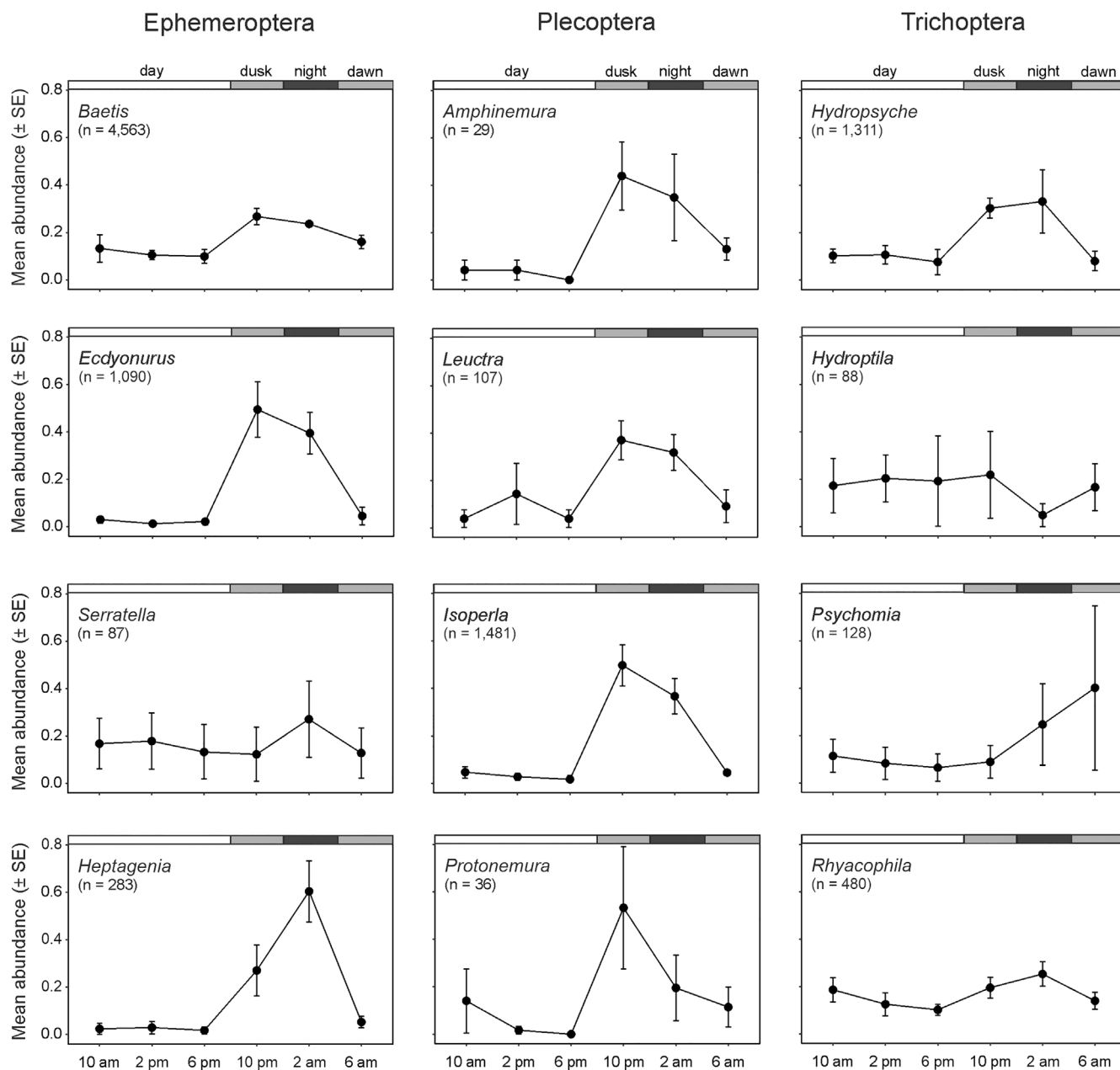
FIGURE 6 Genus specific mean diel abundance ± SD

European grayling is a typical drift feeding species, preying on macro-invertebrates drifting in the water column (Hellawell, 1971). It is thus likely that the high density and diversity of EPT taxa may also favor the high abundance of this threatened fish species in nature-like fish passes.

4.2 | Seasonal and diel distribution

The observed seasonal and diel patterns align with the broad body of knowledge on temporal drift patterns of macroinvertebrates in natural environments (e.g; Allan, 1987; Hansen & Closs, 2007; Rader, 1997; Rincón & Lobón-Cerviá, 1997; Stoneburner & Smock, 1979). Several

studies observed seasonal drift peaks of macroinvertebrates, including high proportions of EPT taxa, in spring and early summer (Allan, 1987; Hansen & Closs, 2007; Stoneburner & Smock, 1979). This matches the observation period of our study, in which the highest drift densities and richest EPT diversity were observed at the beginning of the observation period in April, although drift densities and the overall EPT taxa composition did not change much until the end of the observation period at the end of June. Comparable to many other drift studies, *Baetis* composed the majority of EPT drift (e.g., Allan, 1987; Rincón & Lobón-Cerviá, 1997; Stoneburner & Smock, 1979; Waters, 1965). Consistent with observations of Stoneburner and Smock (1979) in a stream with similar abiotic characteristics to the bypass of our study, the seasonal drift density of this taxon decreased

from April to May followed by an increase in June. However, it should be considered that seasonal drift patterns are taxon- and site-specific and may show interannual variability (Allan, 1987; Hansen & Closs, 2007; Robinson, Tockner, & Burgherr, 2002). Drift of EPT taxa in this study was highest in the first hour after darkness (~22 h), which is in accordance with the conceptional model of Rader (1997), who describes a steep increase in intentional drift entries of macroinvertebrates following decreased light intensity during dusk. Diel periodicity in drift patterns of macroinvertebrates are often an adaptation to the risk of predation, which can be influenced by drift feeding fish that suppress diurnal drift as well as benthic predators that increase nocturnal drift (Huhta, Muotka, & Tikkanen, 2000; Wooster & Sih, 1995).

In addition, accidental drift entries are known to increase during night (Rader, 1997). The results on seasonal and diel drift patterns indicate near-natural living conditions and drift processes for macroinvertebrates in this bypass channel, emphasizing that this restoration measure is successful in restoring lost habitats of the main stream of the River Inn. Especially in heavily modified rivers impacted by multiple stressors and hydropower use, a more comprehensive assessment of ecological effects of both stressors and restoration measures has been proposed (Geist, 2021). The data presented here highlight some of the partly overlooked ecological functions of restoration measures that may be of critical importance for the functioning of these systems, including their food webs.

5 | CONCLUSIONS

As evident from both spatial taxa assemblages and temporal drift patterns in this study, nature-like bypass channels can comprise a rich EPT community that is likely to provide a source function for EPT biodiversity in heavily modified water bodies.

In line with a growing body of knowledge on the habitat function of these restoration measures for fish, nature-like bypass systems not only play an important role in restoring longitudinal connectivity but also in providing compensatory habitats for sensitive aquatic insects. This holds particularly true when it comes to substitution of shallow, fast flowing, and gravely habitats, which are among the habitats most affected by the anthropogenic alteration of rivers. In addition, the controllable nature of these systems allows regular maintenance (e.g., gravel dotation or relocation) in accordance with the site-specific characteristics and the habitat needs of the targeted taxa. Therefore, strategic decisions about the restoration of longitudinal connectivity of streams should favor natural bypass systems to engineered fishways whenever there is sufficient space for their implementation.

AUTHOR CONTRIBUTIONS

Conceptualization: **Christoffer Nagel**, **Juergen Geist**, **Joachim Pander**; Methodology: **Christoffer Nagel**, **Vangelis Mizerakis**, **Juergen Geist**, **Joachim Pander**; Formal analysis: **Christoffer Nagel**; **Vangelis Mizerakis**; Investigation: **Christoffer Nagel**, **Vangelis Mizerakis**; Data curation: **Christoffer Nagel**, **Vangelis Mizerakis**; Writing–original draft:

Christoffer Nagel, **Joachim Pander**, **Vangelis Mizerakis**, **Juergen Geist**.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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