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Patch-scale habitat dynamics: three metrics to assess ecological impacts of frequent hydropeaking

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ABSTRACT

Human activities significantly alter natural river flows, impacting ecosystem functioning and biodiversity worldwide. Hydropeaking, resulting from intermittent on-demand hydropower generation, introduces sub-daily flow fluctuations exceeding natural variability. While the effects of single hydropeaking events are well-studied, the cumulative impacts of frequent hydropeaking requires further exploration. This study aims to develop metrics that captures changes in habitat dynamics at the patch scale (i.e. individual micro-habitats within the habitat mosaic) due to reoccurring hydropeaking. Using hydrodynamic simulations, we introduce three patch-scale metrics to quantify habitat dynamics with high spatial (0.5 m) and temporal (10 min) resolution: (M1) Habitat probability within patches, assessing spatio-temporal diversity of habitats; (M2) Habitat shifts within patches, evaluating habitat persistence for sessile organisms (e.g. vegetation, invertebrates); and (M3) Spatial shifts of habitats, indicating habitat relocation affecting mobile species (e.g. adult fish). Using eight hydro-morphological scenarios representing different levels of anthropogenic modification of flow and morphology, we demonstrate that these metrics effectively quantify changes in habitat dynamics at patch-scale. The results highlight the ecological relevance of these metrics and their potentially utility for river management. By identifying areas susceptible to ecological impacts, these metrics may serve as tools for hydropeaking mitigation, enabling more targeted and spatially explicit habitat management and restoration.

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1. Introduction

In natural river systems, flow variability creates a dynamic mosaic of habitats (see concepts of *patch dynamics* – Townsend 1989; and *shifting habitat mosaic* – Stanford et al. 2005), to which organisms have adapted over millennia (see concepts of *physical habitat template* – Poff and Ward 1990). Human actions, such as flow regulation for hydropower generation (Zarfl et al. 2015; Grill et al. 2019) and simplification of river morphology (e.g. Gregory 2006), have significantly altered these natural dynamics resulting in a significant loss of biodiversity (Lytle and Poff 2004; Ruhi et al. 2018; He et al. 2019; Reid et al. 2019). Hydropower generation, in particular, can profoundly alter the natural flow regime. On the one hand, river reaches affected by flow abstraction experience quasi-constant flow

conditions due to residual flow, with a significant reduction in flow variability and associated disturbance frequency in comparison to natural systems (Robinson 2012; Hayes et al. 2018; Leone et al. 2023; Wechsler et al. 2023). On the other hand, flow regulation and hydropower generation can also intensify flow variability in those reaches where water is returned to the river. In particular, intermittent on-demand hydropower generation causes artificial sub-daily flow fluctuations, known as hydropeaking, that increase flow variability by up to two orders of magnitude as compared to natural systems (Archer and Newson 2002; Halleraker et al. 2022; Burman et al. 2023; Greimel et al. 2016). As the share of volatile renewable energies (i.e. wind and solar) continues to grow, the demand for flexible energy sources is expected to increase (Kougias

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et al. 2019; Gonzalez et al. 2023; Koolen et al. 2023). Consequently, the frequency of hydropeaking will likely rise to compensate for the intermittency of wind and solar power generation and support carbon neutrality.

Over the past three decades, the ecological consequences of hydropeaking have been studied intensively (Moog 1993; Young et al. 2011; Smokorowski 2022; Hayes et al. 2023; Bipa et al. 2024), with a major focus on single hydropeaking events characterized by typical base and peak flows, as well as ramping rates. Many effects have been revealed, such as changes in habitat availability (e.g. Person 2013; Boavida et al. 2015; Holzapfel et al. 2017; Premstaller et al. 2017; Kopecki et al. 2022; Pander et al. 2023; Hauer et al. 2024), organism stranding (e.g. Nagrodski et al. 2012; Auer et al. 2017; Le Coarer et al. 2023; Tonolla et al. 2023; Hayes et al. submitted) and organism drift (Bruno et al. 2016; Aksamit et al. 2021; Schülting et al. 2023; Tonolla et al. 2023). The impact of hydropeaking varies depending on the river morphology; for example, increased morphological complexity generally increases the stranding risks but reduces the risk of drift and habitat alteration (Vanzo et al. 2016).

Various management methodologies and recommendations for hydropeaking mitigation have emerged from these studies (Bruder et al. 2016; Bejarano et al. 2020a; Godinho et al. 2022; Halleraker et al. 2022; Greimel et al. 2023) and legal thresholds have been adopted in national guidelines such as in Switzerland and Austria (Moreira et al. 2019).

More recently, research has increasingly studied the cumulative ecological impacts associated with frequent hydropeaking (see Table 1 for a summary of effects resulting from frequent hydropeaking). For instance, Judes et al. (2023) demonstrated that the frequency of dewatering and shifts to high current velocities over the 15 days preceding sampling influences habitat preferences of invertebrates, but not fish, probably because the latter are able to relocate within the reach in search of suitable habitats. However, Schmutz et al. (2015) emphasized the role of peak frequency as the second most important factor explaining fish community composition and abundance in Austria. Likewise, Hedger et al. (2018) highlighted the cumulative impact of stranding events, related to hydropeaking frequency, on fish abundance and population structure. Additionally, Bruno et al. (2016) illustrated that the first hydropeak after an extended period without peaking resulted in a drastic increase in invertebrate drift rates whereas subsequent daily hydropeaking events exhibited significantly lower drift rates.

Many ecological impacts associated with hydropeaking, as mentioned above, may be related to the frequency (i.e. reoccurrence) of abrupt shifts in habitat conditions or, more broadly, to the increase in overall habitat dynamics and to the organism's mobility (Shea and Peterson 2007; Bätz et al. 2023). In other words, the impact of the hydropeaking hydrology on organisms is mediated through changes in hydraulic conditions (e.g. water depth and current velocities) and associated habitats, alongside the organisms' capacity to react/resist to these changes (see Table 1). For instance, increased habitat dynamics can lead to more frequent drying of habitats and subsequent stranding events, affecting particularly more sessile species and life stages (e.g. invertebrates; Perry and Perry 1986; Kennedy et al. 2016; Miller et al. 2020; Tonolla et al. 2023). Conversely, species and life stages with higher mobility (e.g. adult fish), may need to constantly relocate in search for suitable habitats (Kraft 1972; Bunt et al. 1999; Berland et al. 2004; Murchie and Smokorowski 2004; Heggenes et al. 2007; Scruton et al. 2008; Taylor and Cooke 2012; Boavida et al. 2017; Capra et al. 2017; Lenormand et al. 2021), which could have significant consequences on their energy budgets (Lauters et al. 1996; Lagarrigue et al. 2002; Flodmark et al. 2006; Scruton et al. 2008; Puffer et al. 2015; Rocaspana et al. 2016; Kelly et al. 2017; Puffer et al. 2017). However, significant gaps remain in our understanding of these dynamics and the adaptive responses of different organisms. Furthermore, the practical management of spatio-temporal changes in habitat dynamics due to anthropogenic flow alterations, such as hydropeaking, remains a challenge.

This paper aims to address this gap by introducing three metrics designed to quantify habitat dynamics at the patch scale (i.e. individual microhabitats within the habitat mosaic; Frissell et al. 1986), with a particular focus on the influence of hydropeaking frequency on the complex interaction between flow regime and river morphology. By using 2D hydrodynamic simulations, these metrics offer a spatially explicit analysis of the impacts of hydropeaking on habitat dynamics, complementing existing reach scale approaches (e.g. habitat duration curve; Bovee 1982; Capra et al. 1995; Valentin et al. 1996; Bowen et al. 1998; Parasiewicz et al. 1998; Freeman et al. 2001). We evaluate the extent to which these metrics can quantify habitat dynamics at the patch scale using a set of hydro-morphological scenarios. These hydro-morphological scenarios combine two different flow regimes (natural and hydropeaking) with a gradient of morphologies of varying complexity (braided, groynes-controlled, alternating bars, channelized), representing different

Table 1. Effects related to increased habitat dynamics due to recurring hydropeaking on different organism groups as reported in the literature. Main links to the three patch-scale metrics presented in the article are indicated with a cross in the three columns at the right, with M1 = habitat probability within patches, M2 = habitat shifts within patches, and M3 = spatial shifts of habitats. The most relevant metrics are indicated with bold crosses.

Effects related to increased habitat dynamics due to frequent hydropeaking			Relevant metric		
			M1	M2	M3
Vegetation	Community/Population	Frequent hydropeaks alter the natural gradient of riverine vegetation, transitioning from consistently wetted aquatic plants to flood-intolerant riparian species (Bejarano et al. 2018, 2020b). Establishment of pioneer vegetation is reduced (Tonolla et al. 2021).	x	X	
	Germination/Growth	Pioneer riparian vegetation and aquatic plants experience reduced germination and growth, and increased mortality due to frequent wetting and drying (Bejarano et al. 2018, 2020b).	x	X	
Invertebrates	Biomass/Density	Benthic invertebrate density in near-shore habitats correlates negatively with the frequency of flow fluctuations (Perry and Perry 1986), which may result in an up to 85% decrease in biomass (Parasiewicz et al. 1998).	X	X	
	Habitat	Due to the limited availability of persistent habitats (Perry and Perry 1986; Tanno 2012; Person 2013), macroinvertebrates in hydropeaking rivers differ in their habitat preferences from conspecifics in non-regulated rivers and depend on the interplay between current microhabitat hydraulics and the hydraulic conditions of the preceding 15 days (Judes et al. 2023).	X	X	
	Drift	Macroinvertebrates, and especially those preferring lentic habitats, exhibit increased passive (i.e. involuntary) drift due to abrupt increases in current velocity and bed shear stress (Brittain and Eikeland 1988; Gibbins et al. 2007; Naman et al. 2016; Schülting et al. 2023; Tonolla et al. 2023). The first hydropeak triggers the most significant drift response, with subsequent peaks inducing smaller but noteworthy changes in drift composition (Irvine 1985; Irvine and Scott 1988; Bruno et al. 2016).	x	X	
	Stranding	Stranding risk is generally linked to the flow ratio and associated expansion and contraction of the dewatering zone (Perry and Perry 1986; Tanno et al. 2021; Tonolla et al. 2023). Dewatering of >1 consecutive hour reduces the viability of aquatic insects' eggs by 80–98% (Kennedy et al. 2016; Miller et al. 2020).		X	
Fish	Community/ Population	Channel habitat complexity and the number of hydropeaks per year with a high flow ratio best explain the integrity of the fish community, with a frequency of >20 high hydropeaks per year leading to a degradation of the population structure and community composition (Schmutz et al. 2015).	x	x	X
	Habitat	Hydropeaking significantly reduces persistent habitat area (Bovee 1982; Valentin et al. 1996; Bowen et al. 1998; Freeman et al. 2001; Bartoń et al. 2022; Jelovica et al. 2023). According to Person (2013) only 5% of spawning habitats and 30% of YOY brown trout habitats were persistent, whereas 60–65% of the habitats were prone to dewatering and highly suitable habitats displaced. Reduced habitat persistence prompts increased relocation of fish to follow their preferred habitats (Jelovica et al. 2023; Judes et al. 2023). Juvenile trout and adult grayling have been shown to exhibit a low success rate (probability <0.4) in locating suitable habitats during hydropeaking up-ramping (Jelovica et al. 2023). Relocation of fish can be reduced in the presence of cover, such as debris and vegetation (Valentin et al. 1996; Parasiewicz et al. 1998; Bunt et al. 1999; Rato et al. 2021), in pool habitats (Kraft 1972; Parasiewicz et al. 1998; Bunt et al. 1999; Walker and Adams 2016; Boavida et al. 2017) and potentially due to individual learning (Capra et al. 2017).	X	X	X
	Movement	Studies revealed varied fish movement, with some species exhibiting strong site fidelity (especially salmonids) and others relocating over considerable distances (Kraft 1972; Bunt et al. 1999; Berland et al. 2004; Murchie and Smokorowski 2004; Heggenes et al. 2007; Scruton et al. 2008; Taylor and Cooke 2012; Boavida et al. 2017; Capra et al. 2017; Lenormand et al. 2021). However, fish in hydropeaking rivers generally show larger home and core ranges compared to those in unregulated rivers. For instance, Rocaspana et al. (2019) observed adult brown trout to increase their mean home range from 112.1m (range 73.2–224.5m) under near-natural flow to 237.9m (82.5–568.9m) with hydropeaking. Similarly, Alexandre et al. (2016) found a significant positive correlation between the distance from core range and the number of hydropeaks for Barbel.			X
	Energy demands	Given that energy demands for swimming increase exponentially with current velocity (McKenzie 2011), hydropeaking likely raises demands. Higher energy demand may not always meet food availability (Lauters et al. 1996; Lagarrigue et al. 2002; Flodmark et al. 2006; Scruton et al. 2008; Rocaspana et al. 2016; Kelly et al. 2017). For instance, Puffer et al. (2015, 2017) showed that hydropeaking can lead to a 10% decrease in growth rate and a 16% reduction in body fat for juvenile Atlantic Salmon.	X	X	X
	Stranding	Repeated flow fluctuations due to hydropeaking exceeding natural thresholds can lead to significant stranding in dewatered zones, particularly of eggs, larvae and fry (Connor and Pflug 2004; Young et al. 2011; Nagrodski et al. 2012; Hauer et al. 2014; Auer et al. 2017; Hedger et al. 2018; Auer et al. 2023; Le Coarer et al. 2023; Führer et al. 2024; Hayes et al. 2024, submitted). Pander et al. (2023) observed an 80% mortality rate for eggs and almost 100% mortality rate for brown trout larvae due to shifting habitat conditions in a hydropeaking reach, as compared to 55–63% and 80–85% mortality, respectively, in unregulated reaches. During peak flow, high current velocities can increase the risk of egg detachment from the substrate (Bartoń et al. 2021). Bauersfeld (1977) estimated a 1.5% fry loss per hydropeak due to stranding, summing up to a 59% loss of salmon fry for one season. However, stranding may be strongest after long periods without hydropeaking, as demonstrated by Halleraker et al. (2003), who found that significantly more brown trout fry were stranded in the first dewatering event (mean = 22%) compared to the second to fifth event (mean = 10%).	X	X	X

levels of anthropogenic modification. We then discuss the ecological relevance of each metric and demonstrate their potential utility in assisting river managers with spatially explicit planning of mitigation measures at the patch-scale. Finally, we explore potential directions for future research to further validate and refine the metrics.

2. Methods

An overview of the workflow and applied methodology is given in [Figure 1](#). We used the flow time-series of a natural and a hydropeaking flow regime and conducted 2D hydrodynamic simulations (BASEMENT, Version 2.8.2) for four river reaches following a gradient of morphological complexity (i.e. braided, groynes-controlled, alternating bars, channelized) to derive the spatial distribution of flow depth and current velocity. These two hydraulic variables were then employed to define ecologically relevant physical habitats for all hydrodynamic simulations based on unsupervised clustering. By combining the two flow time-series (representing the temporal dynamics) with the physical habitat classification of the four considered morphologies (representing the spatial dynamics), we were able to build time-series of physical habitat distributions for eight hydro-morphological scenarios. These physical habitat distribution time-series served as basis for calculating the three metrics for each hydro-morphological scenarios. Except for the hydrodynamic simulations, all analyses were performed using R-packages and programming language.

The following subsections provide a more detailed description of the various steps illustrated in [Figure 1](#). The presented test case is instrumental in developing hydro-morphological scenarios along gradients of anthropogenic modification. These scenarios illustrate the applicability and versatility of the metrics in capturing the complex interplay between flow regimes and river morphology in defining habitat dynamics at the patch scale.

2.1. Flow time-series

Two contrasting flow time-series, representing a hydropeaking regime (high flow fluctuations) and a natural regime (low flow fluctuations), each with a temporal resolution of 10 min, were available for developing the hydro-morphological scenarios. This high temporal resolution allows for a detailed and accurate representation of the rapid and frequent flow fluctuations caused by hydropeaking. The flow time-series for the hydropeaking regime was retrieved from gauging station ID 2019 of the Aare

River in Switzerland (FOEN 2020). The flow time-series for the natural regime was obtained from gauging station ID 2109 of the neighbouring Lütschine River (FOEN 2020). The catchments of the two river systems are comparable regarding glacier cover, average elevation, hydrology and related susceptibility to meteorological events (Bätz et al. 2023). The hydropeaking regime of the Aare River is representative of Alpine rivers used for intermittent hydropower generation (see comparison in Carolli et al. 2015). During winter, it is characterized by several daily hydropeaks with typical base flows of $3.1 \text{ m}^3/\text{s}$ and peak flows of $49.1 \text{ m}^3/\text{s}$ (Person 2013; Tonolla et al. 2017).

In the hydro-morphological scenarios, we focus on the winter season from December to February covering 11 years (2010–2021; see example in [Figure 1](#)). For the Aare River, winter is the period when hydropeaking is most pronounced, whereas the flow in the Lütschine River is fairly stable and generally low. Furthermore, key ecological processes occur during this period such as trout early development (Tonolla et al. 2017). To allow for a more direct comparison of the two time-series, the flow data from the Lütschine River were multiplied by 1.46, corresponding to the size ratio between the two catchment areas.

To minimize the impact of short flow fluctuations (10-minute intervals) and measurement noise (e.g. slight variations in flow) on the physical habitat distribution time-series, we applied a weighted moving window (weights 1, 2, 3, 2, 1). This method applies a 50-minute smoothing to the data, which may seem long but is intended to enhance the representation of central values while minimizing the impact of peripheral ones. Preliminary tests indicated that this smoothing technique, which has also been applied in other studies (e.g. Zimmerman et al. 2010; Bevelhimer et al. 2015; Bejarano et al. 2020a), did not significantly alter the results of the metrics. This approach captures ecologically significant changes in habitat conditions associated with hydropeaking events while filtering out minor flow fluctuations that lack substantial ecological impact, ensuring the stability and reliability of the habitat dynamics analysis.

2.2. Morphologies and hydrodynamic simulations

Four distinct morphologies, representing a gradient of morphological complexity (i.e. braided, groynes-controlled, alternating bars and channelized) were used alongside the contrasting flow regimes presented above to develop comprehensive hydro-morphological scenarios. These morphologies are

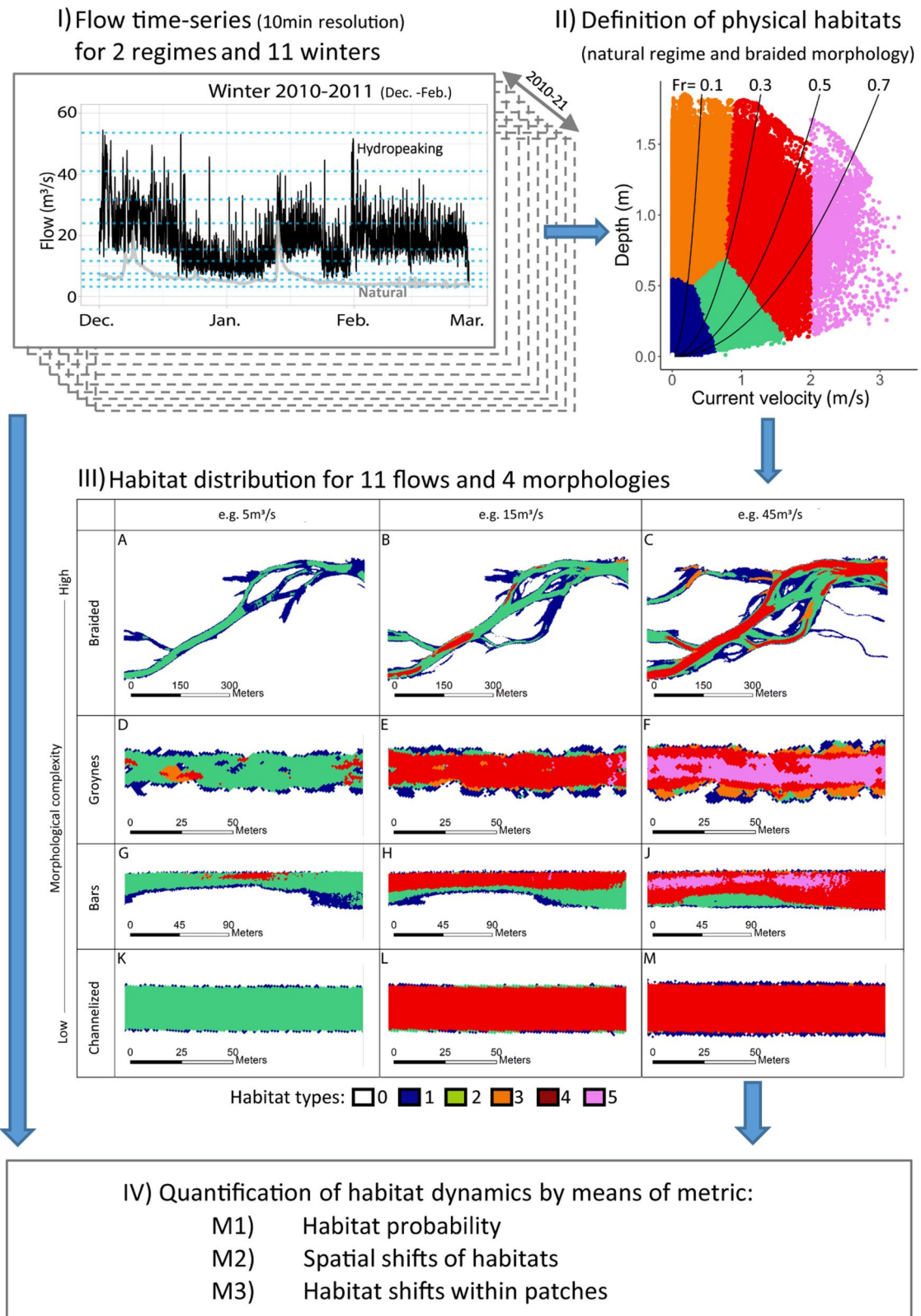


Figure 1. Workflow for deriving the metrics for habitat dynamics at patch-scale. The approach includes: (I) Flow time-series of the natural and the hydropeaking flow regimes, with an example for winter 2010–11. (II) Definition of five physical habitat types based on current velocity and flow depth, with Fr indicating the isoFroude lines. (III) Habitat distribution of the hydrodynamic simulations, with examples for all four morphologies. The selected flows correspond to the Q25, Q50, and Q75 of the natural winter flows, as well as to the approximate minimum and maximum flows of a typical winter hydropeak (3.1 and 49.1 m³/s). Note the differences scales in the maps refer only to the scale of representation and not to the modeling itself. (IV) By combining the flow time-series with the habitat classification of the four morphologies at different flows, the habitat dynamics at the patch scale can be quantified using the three metrics.

typical for rivers impacted by hydropeaking in alpine systems (e.g. Vanzo et al. 2016). The groynes-controlled (550 m long, about 35–18 m wide), alternating bars (1,225 m long, about 32–38 m wide) and channelized (1,100 m long, about 31 m wide) reaches represent the topography of the Aare River near Innertkirchen, Switzerland. To represent the topography in detail the three reaches were surveyed by an Unmanned Aerial Vehicle (UAV) at low flow and the images were photogrammetrically processed to derive high resolution data of the topography. The braided morphology (2,650 m long, about 340–145 m wide) was sourced from the Ashley River in New Zealand (LINZ Data Service under the Creative Commons Attribution 4.0 International license). This section of the Ashley River was chosen as a morphological analogue for the Aare River's pre-altered state, based on similarities in hydrology but also historical channel width, as evidenced by historical mappings of the Aare River from 1764 (Zaugg 2015). The lengths of all reaches were deemed sufficient to effectively represent the diversity of the river's morphological structures, which form the habitat templates and typically range from 1 to 10 times the channel width.

Hydrodynamic simulations of the four morphologies were conducted (BASEMENT, Version 2.8.2) following standard protocols for input data preparation, calibration and validation. The resolution of the unstructured triangular mesh representing the topography of each reach was determined by the morphological complexity. Using the tool BASEmesh, zones within the simulated reaches with greater complexity were assigned finer triangular mesh (minimum size of 0.1 m^2), while less complex zones (e.g. mostly flat and elevated parts of floodplains only partially inundated for the tested flows), were represented with coarser triangular mesh (maximal size of 15 m^2). This approach balanced computational efficiency with the need to capture hydraulic variations (e.g. eddies) across different flow conditions and riverbed macro-structures (e.g. Vanzo et al. 2021). For instance, the smallest morphological structures, such as clusters of block stones approximately 3 m in diameter, were effectively represented. Bürgler et al. (2023) conducted a comparative analysis demonstrating the reliability of the mesh resolutions used in this study for similar river morphologies, with mesh sizes ranging from 0.5 to 27 m^2 , thus supporting our chosen approach.

Results for the groynes-controlled, alternating bars and channelized morphology reaches were extracted from a single simulation of the 16 km-long river segment of the Aare River affected by hydropeaking. Calibration was based on point measurements (using Acoustic Doppler Current Profiler,

ADCP) of flow depths and current velocities across various flow conditions. This calibration process allowed for refining the uniform roughness coefficient, which was iteratively adjusted to minimize the Root Mean Square Error (RMSE) and achieve an optimal fit with the observed data. Validation of the simulations was accomplished by comparing simulated wetted areas with those derived from UAV-based aerial imagery, demonstrating a high degree of accuracy in the simulations.

Given the strong morphological parallels between the braided sections of the Ashley River and the historical Aare River (as discussed at the beginning of this chapter), and the absence of specific calibration and validation data for the braided morphology, we applied the simulation parameters from the 16 km-long Aare River segment to the simulations of the braided morphology. Despite this approximation, the simulations effectively capture the flow conditions across the four analyzed morphologies, offering a reliable and comparable basis for the development of hydro-morphological scenarios.

Simulations were performed over a spectrum of 11 steady flows (2.5, 3.5, 5.0, 10.0, 15.0, 25.0, 35.0, 45.0, 60.0, 80.0 and $120.0 \text{ m}^3/\text{s}$). These 11 flows were selected based on the frequency distribution observed over the study period, spanning from the 5th percentile in winter to the 95th percentile in summer. In addition, the selection of the flows was based on the responsiveness of the four morphologies, particularly in terms of wetted width expansion, as more rapid hydraulic variations occur at low flows. These selection criteria ensure that the simulations capture the complex interplay between flow regime and morphological complexity across the hydro-morphological scenarios.

To streamline subsequent processing in R, the results from the hydrodynamic simulation (water depth and current velocity) were interpolated into a uniform raster with a resolution of $0.5 \times 0.5 \text{ m}$. This resolution is sufficient to capture local variations in habitat dynamics, including micro-habitats, and relevant for aquatic organism such as fish, invertebrates and vegetation.

2.3. Habitat definition and classification

We focus on physical habitats at the patch scale, corresponding to individual micro-habitats within the habitat mosaic (Frissell et al. 1986). This scale, represented by a single pixel of the raster ($0.5 \times 0.5 \text{ m}$), serves as the fundamental unitary element of our analysis. The patch scale is particularly suitable for capturing local variations in habitat dynamics, which are critical for understanding the impacts of anthropogenic modifications, such as

hydropeaking, on aquatic organisms typically considered in river management (e.g. EU Water Framework Directive, Swiss Water Protection Act), including fish, invertebrates and vegetation (Table 1). By focusing on this scale, our analysis remains directly relevant to key ecological processes (i.e. habitat disturbance, temporal dynamics and refugia) and behaviors of aquatic organism such as fish movement, invertebrate colonization and plant establishment (e.g. Frissell et al. 1986; Lancaster and Hildrew 1993a, 1993b; Palmer et al. 2000; Shea and Peterson 2007; McKenzie 2011; Bejarano et al. 2018; Mathers et al. 2022).

To maintain methodological simplicity and clarity, we concentrated on water depth and current velocity for physical habitat definition, intentionally excluding other variables (e.g. temperature, instream cover, substrate composition). Furthermore, by focusing on physical habitats, we intentionally excluded biological, taxa-oriented criteria (e.g. based on habitat preference of taxa) for habitat classification, to demonstrate the broad applicability of our patch-scale metrics across a diverse range of organisms with varying levels of mobility (sessile versus mobile organisms, *sensu* Bätz et al. 2023). However, the methodology applied here (Figure 1) can be easily adapted to a species-based habitat classification by incorporating taxa-specific preference curves, thus allowing a more targeted evaluation of the habitat dynamics via the metrics presented below.

A unique definition of physical habitat was derived from the simulated current velocity and water depth across all 11 flows (Figure 1; Chapter 2.2). We applied an unsupervised clustering method (similar to van Rooijen et al. 2021 or Farò et al. 2022), using a weighted k-means clustering algorithm (SWKM R-package; Zhang et al. 2020), to a reference “natural scenario” defined by the natural flow regime (Chapter 2.1) and braided morphology (Chapters 2.2). To account for interannual variability across flow time-series, i.e. the different cumulative durations of each of the 11 considered flows, we assigned weights to each simulated flow based on its hydrological likelihood of occurrence. The algorithm was constrained to identify four physical

habitats based on ecologically relevant boundary conditions: current velocities <2.00 m/s and water depth >0.01 m. Moreover, we enforced two additional clusters to represent extreme (i.e. unsuitable) physical habitats, having either current velocities >2.00 m/s (high current velocities) or water depths <0.01 m (dry conditions).

These physical habitats were then applied to the other seven hydro-morphological scenarios. A selection of the resulting classified simulation at different flows for the four morphologies is presented in Figure 1. In addition, detailed plots showing the availability of each physical habitat type across the four morphologies and 11 flows are shown in the supplementary material (S 1).

Overall, the physical habitat types 1–4 defined in this study align with those identified by other research using similar methods and hydraulic variables (e.g. Hauer et al. 2009; Wyrick et al. 2014; van Rooijen et al. 2021; Wegscheider et al. 2022). For example, physical habitat types 2 and 4 (Figure 1) have Froude numbers typically found in riffles whereas physical habitat type 3 has Froude numbers typically found in pools, according to the classification of Jowett 1993. Table 2 provides a description and indication of the potential ecological relevance of the defined physical habitat types. While this alignment suggests the potential generality and ecological validity of the physical habitats defined here, the innovation of our approach lies in the use of these to calculate the patch-scale metrics (Chapter 3).

2.4. Habitat time-series

We modified the reach-scale time-series analysis originally proposed by Capra et al. (1995) to quantify habitat dynamics at the scale of a single habitat patch (i.e. for each raster cell) for each hydro-morphological scenario. This involved combining the two flow time-series (natural and hydropeaking regime) with the physical habitat classification of the four morphologies for each of the 11 flows. In other words, we employed the flow time-series to retrieve the physical habitat distribution for the

Table 2. Habitat types (see definition in Figure 1), their physical characteristics and potential ecological relevance (based on (Lamouroux and Souchon 2002; Dolédec et al. 2007)). The colours correspond to the habitat types shown in Figure 1, Figure 2 and Figure 3.

Habitat type Nr.	Label	Physical characteristics	Potential ecological relevance
0	Dry	Not wetted	Risk of stranding
1	Shallow	Shallow water depth Slow current velocity	Habitat provision for many young fish stages
2	Shallow-medium current	Shallow water depth Medium current velocity	Habitat provision for small rheophilic fish, young brown trout and many mayflies
3	Deep-slow current	High water depth Low current velocity	Habitat provision for limnophilic taxa, adult brown trout and some molluscs
4	Fast current	Medium to fast current velocity	Habitat provision for rheophilic specialists such as adult grayling and most simuliids
5	Very fast current	Very fast current velocity	Risk of drift

respective flow and morphology to build a time-series of physical habitat. This resulted in a physical habitat time-series for each of the eight hydro-morphological scenarios, which served as the basis for calculating the metrics. Each scenario can be conceptualized and plotted along two gradients of anthropogenic modification: the frequency of flow fluctuations, with natural flow fluctuations being less pronounced than those under hydropeaking, and the degree of morphological complexity, with the channelized morphology exhibiting lower complexity compared to braided morphology.

The spatio-temporal resolution (0.5×0.5 m cells and 10-minute intervals) is deemed sufficient to accurately represent the dynamics of habitat patches, as it effectively represents the impact of flow fluctuations (Chapter 2.1) and varying morphological complexity on hydraulic conditions (Chapter 2.2) and the resulting changes in physical habitats (Chapter 2.3). While other similar approaches at the reach scale exist (e.g. Bovee 1982; Capra et al. 1995; Valentin et al. 1996; Bowen et al. 1998; Parasiewicz et al. 1998; Freeman et al. 2001), the here proposed methodology evaluates habitat dynamics at a higher spatial resolution, specifically focusing on the dynamics of individual habitat patches.

Specifically, we defined flow ranges to combine the flow time-series with the physical habitat distribution. Each flow range was delimited by the central value between two adjacent flows of the 11 simulated flows (i.e. <3.00 , $3.00-4.25$, $4.25-7.50$, $7.50-12.50$, $12.50-20.00$, $20.00-30.00$, $30.00-40.00$, $40.00-52.50$, $52.50-70.00$, $70.00-100.00$, >100.00 m³/s). For each flow range, the corresponding physical habitat distribution was then assigned (i.e. physical habitat classification for 15.00 m³/s for any flows within the flow range $12.50-20.00$ m³/s), assuming that it was representative for the entire flow range. This discretization into flows ranges served as basis to expand the approach proposed in Bätz et al. (2023) and develop patch-scale metrics to quantify the habitat dynamics for the eight hydro-morphological scenarios.

3. Metric description and computation

The three metrics presented in this study rely on 2D habitat modeling and are calculated using sub-hourly time-series of physical habitat distributions (10 min temporal resolution in this case), as illustrated in the methods above. The metrics are designed to quantify the habitat dynamics at the patch scale, which corresponds to individual microhabitats (0.5×0.5 m) within a larger habitat mosaic.

We use the term “metrics” to highlight their utility in quantifying the impact of hydropeaking on

habitat dynamics, particularly in a management context. However, the three metrics can also be employed as habitat descriptors, in both natural or anthropogenically modified river systems, to capture the characteristics of a habitat patch in terms of its dynamic state or persistence (e.g. a patch can exhibit certain habitat type(s) and the associated dynamics or persistence over time).

3.1. M1: Habitat probability within patches

Habitat probability within patches measures the likelihood of different habitat conditions within a patch due to temporal flow changes (Bätz et al. 2023; Figure 2). This metric reflects the duration of occurrence of each specific habitat type within each patch, thereby identifying dominant habitat types based on their cumulative duration over the considered period. The habitat mosaic is shifting in response to the changing flow (Stanford et al. 2005), with some patches of the habitat mosaic exhibiting a more pronounced response than others (e.g. Lancaster and Hildrew 1993a, 1993b; Shea and Peterson 2007; Weber et al. 2013; Strom et al. 2016; Hauer et al. 2024). By expressing habitat availability and distribution as patch-specific probabilities, the here proposed metric provides an accurate representation of the dynamic conditions that organisms may experience in a patch under hydropeaking.

Habitat probability within patches offers valuable insights into the spatio-temporal diversity of habitats, providing a realistic assessment of habitat dynamics with ecological relevance (see potential relevance of this metric in Table 1). While our focus remains on physical habitats rather than directly linking these probabilities to organism presence, this metric still provides meaningful insights into habitat dynamics with significant ecological implications. For instance, riparian vegetation, although tolerant of inundation, requires a balance of habitat conditions that are not excessively wet or dry for successful growth and establishment (Bejarano et al. 2018, 2020b). This metric therefore, complements the other two patch-scale metrics below by providing patch specific probability of finding the various considered habitat types over time.

To compute this metric, the duration of occurrence of each specific habitat type within each patch (i.e. individual cell) in the time-series of physical habitats for each hydro-morphological scenario was summed (see example in Figure 2). By dividing the counts (i.e. cumulative duration) by the total time of the flow time-series, a patch specific probability for each habitat type was derived. The probability for each habitat type ranges from 0 (= lowest likelihood) to 1 (= highest likelihood), while the sum of

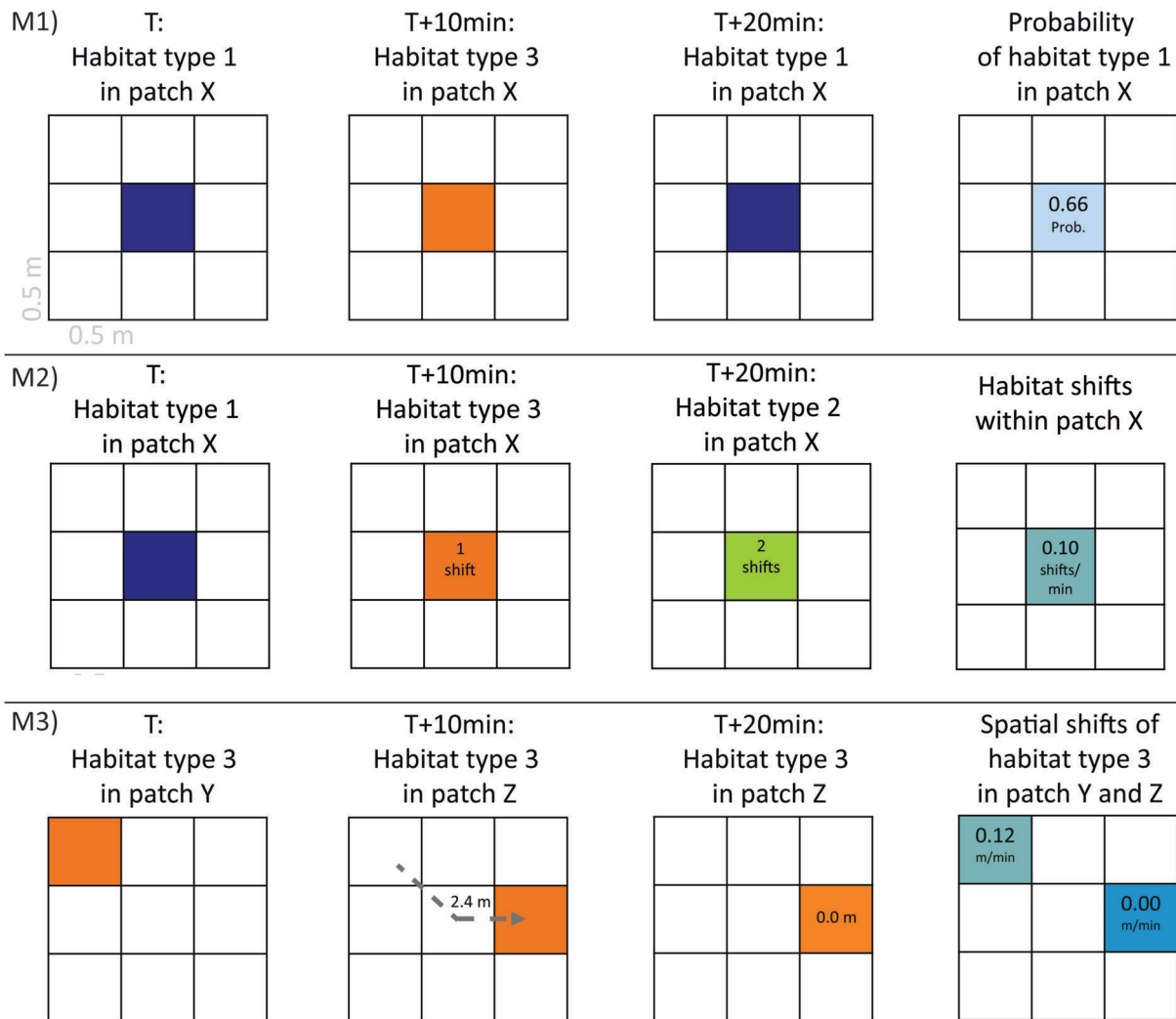


Figure 2. Schematic example illustrating the calculation of the metrics. M1 = habitat probability within patches: If patch X represents habitat type 1 at time-step T, habitat type 3 at T + 10 minutes and habitat type 1 at T + 20 minutes, then patch X has a 0.66 probability of being habitat type 1 over the specified 20-minute time interval. M2 = habitat shifts within patches: If patch X represents habitat type 1 at time-step T, habitat type 3 at T + 10 minutes and habitat type 2 at T + 20 minutes, then patch X experienced a habitat shift of 0.10 shifts/min over the specified 20-minute time interval. M3 = spatial shifts of habitats: Habitat type 3 is located in patch Y at time-step T and in patch Z at T + 10 minutes and T + 20 minutes. Accordingly, patch Y and Z experienced a spatial shift of habitat of 0.12 and 0.00 m/min, respectively, over the specified 20-minute time interval.

the probabilities for each patch over all six habitat types consistently equals to 1.

To elaborate further, we specifically determined the frequency of occurrence of each flow range within the two regime scenarios (natural or hydro-peaking). This allowed attributing occurrences to the simulated habitat distributions for each hydro-morphological scenario and extracting the proportion of time that a patch (i.e. cell) was assigned to a particular habitat type over duration of the flow time-series (11 winters, with a 10-minute resolution).

3.2. M2: Habitat shifts within patches

The metric of habitat shifts within patches tracks the number of times (i.e. frequency) that habitat conditions change in a patch over a period of time (Bätz et al. 2023; Figure 2). This metric evaluates habitat

persistence and is therefore especially valuable for organisms with limited mobility, such as plants and most macroinvertebrate taxa that have to cope with the changing habitat conditions in a specific location on a given patch. The metrics also includes shifts to dry conditions, which may lead to stranding, or to high current velocities that may cause organism drift (see potential relevance of this metric in Table 1). For instance, frequent habitat shifts within near-shore patches have been shown to negatively impact benthic invertebrate density (Perry and Perry 1986), potentially leading to an up to 85% decrease in biomass (Parasiewicz et al. 1998).

To compute this metric, the shifts from one habitat type to another habitat type at the next time-step were counted for each patch (i.e. individual cell) throughout the entire flow time-series. The total number of counts was divided by the duration of

the flow time-series, resulting in the average number of habitat shifts within each patch. The number of habitat shifts within each patch ranges from 0 (= no habitat shift) to the maximum number of time steps of the flow time-series (= if a patch exhibits a shift in habitat type at each time step).

For each time-series of physical habitats and hydro-morphological scenarios, the number of times a cell changed habitat type was recorded. The total number of habitat shifts was divided by the duration of the flow time-series (11 winters, with a 10 min resolution), resulting in the average number of habitat shifts over time. This metric allows three different types of shift to be quantified, considering that habitat shifts towards the extreme habitats (0, 5) have particular ecological meaning:

- i. Habitat shifts between habitat types 1–4 (excluding shifts to the extreme habitats 0 and 5) indicate the dynamic habitat conditions organisms face when persisting in a patch over the whole period (Southwood 1977; Bovee 1982; Capra et al. 1995; Valentin et al. 1996; Bowen et al. 1998; Parasiewicz et al. 1998; Freeman et al. 2001; Bätz et al. 2023).
- ii. Habitat shifts to habitat type 0, calculated over the entire period, indicate the frequency of drying and, thus, the potential for stranding events for organisms present in a patch. Other aspects involved in stranding such as rate of dewatering are not considered (e.g. Young et al. 2011; Nagrodski et al. 2012; Hayes et al. submitted).
- iii. Habitat shifts to habitat type 5, calculated over the entire period, reflect the frequency of increases in current velocities and, thus, the potential for drifting events for organisms present in a patch. Note that this metric only assesses the frequency of drifting events in a general way as habitat use for current velocity >2m/s is uncommon for many taxa (e.g. Plichard et al. 2020; Forcellini et al. 2022).

3.3. M3: Spatial shifts of habitats

Spatial shifts of habitats reflect the extent to which habitats of a given type change their position due to changes in flow over time (Bätz et al. 2023; Figure 2). This metric is particularly valuable for mobile organisms, like juvenile and adult fish, which are forced to relocate in response to changes in habitat spatial distribution due to the fluctuating flow (see potential relevance of this metric in Table 1). For instance, Rocaspana et al. (2019) observed that adult brown trout increased their mean home range from 112.1 m (range 73.2–224.5m) under near-natural flow to 237.9 m (82.5–568.9m) under

hydropeaking conditions, likely due to the increased spatial shifts of their preferred habitats.

To calculate this metric, we measured the distance with the lowest associated costs (i.e. the easiest path; see below) to move between a patch of a specific habitat type and a patch of the same habitat type at the subsequent time step. The distances of all time steps over the entire flow time-series were summed up. The sum was divided by the duration of the flow time-series, resulting in the average number of spatial shifts for each patch per time. For a given patch, the spatial shifts of habitats ranges from 0 (= no spatial shift) to the largest potential path between two cells within the simulated domain.

We employed the FiER tool (Fish Escaping Routes tool) developed by Lüthy (2021), which uses habitat type, current velocity and water depth to calculate, for each patch (i.e. raster cell), the lowest cost path to a patch with the same habitat type at a different flow. The lowest cost path is determined by the shortest distance between the two patches while excluding areas with water depth <0.01 m (habitat type 0=dry) and current velocity >2.00 m/s (habitat type 5=high current velocity). For each physical habitat classifications (=11 flows × 4 morphologies), these paths were computed for each habitat type between two adjacent flow ranges in both upward (from lower to higher flow ranges) and downward (from higher to lower flow ranges) directions. Whenever the flow time-series (natural or hydropeaking) indicated a change in flow range, the habitat-specific displacements (i.e. from one raster cell to another) between the two flow ranges were then summed for each cell for the desired hydro-morphological scenario. Finally, we computed the average displacement per day for each habitat type by dividing the total displacement by the duration of the flow time-series (11 winters, with a 10-minute resolution).

4. Results on metrics performance

The following chapters provide an example of how the three metrics presented above are applied to eight hydro-morphological scenarios to illustrate their ability to quantify the complex interplay between flow regimes and river morphology on habitat dynamics at the patch scale.

4.1. M1: Habitat probability within patches

We display the most probable or dominant physical habitat type among types 1, 2, 3 and 4 for each hydro-morphological scenario in Figure 3.

Hydropeaking generally leads to a change in the dominant physical habitat type within the main channel, as reflected in a high probability of physical habitat

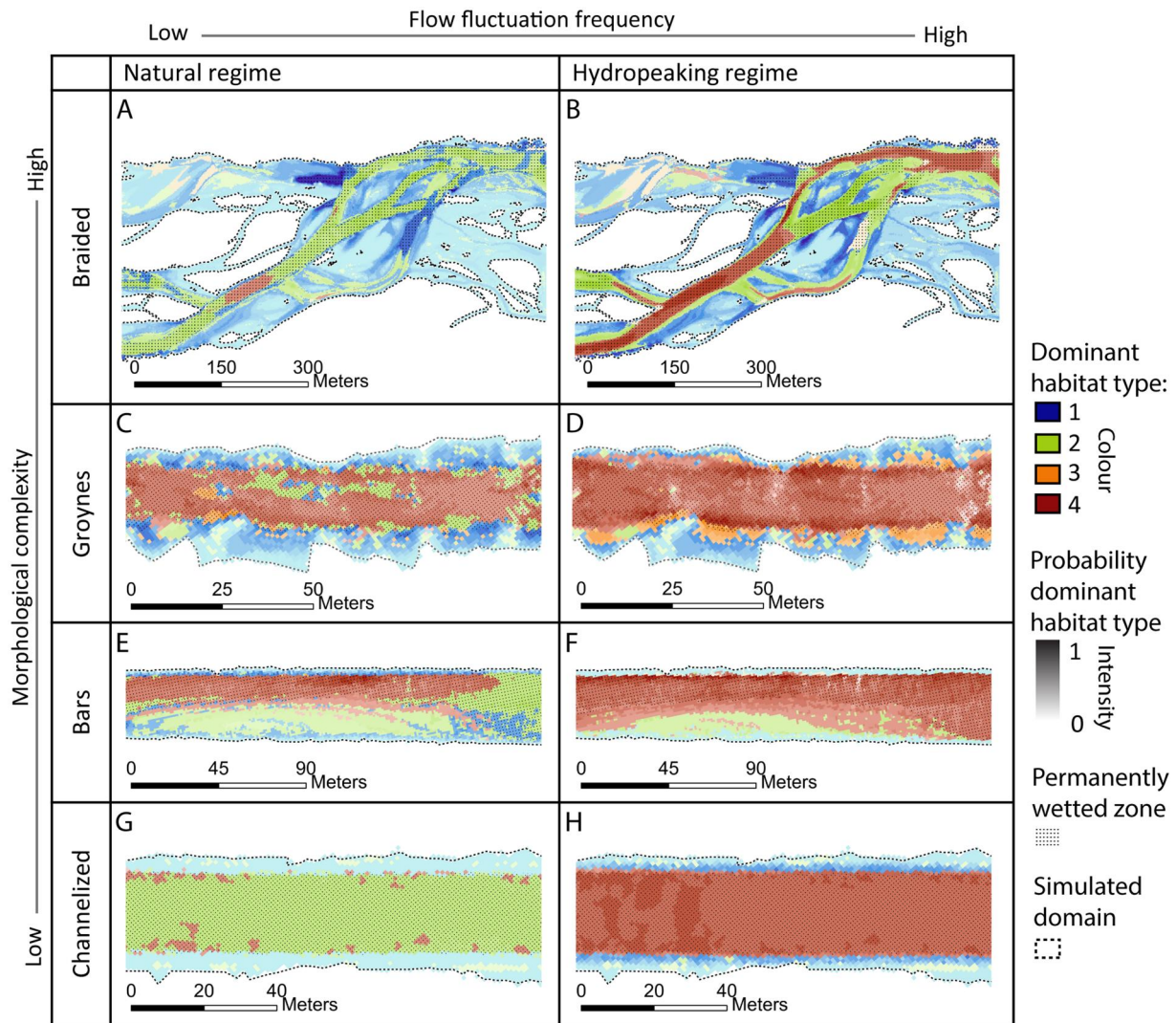


Figure 3. Time-integrated distribution of the dominant (physical) habitat type for each of the eight hydromorphological scenarios. The colours represent the four habitat types 1–4, while the colour intensity indicates the related probability. For example, a probability of 0.8 for the dominant habitat type 4 indicates that this habitat type is the most frequently occurring one in that specific location, persisting for 80% of the duration of the analysed time-series. The maximum inundated area corresponds to the area inundated at the maximum discharge of $120.0 \text{ m}^3/\text{s}$. Note the different scales of representation between morphologies.

type 2 in the natural regime, compared to physical habitat type 4 under hydropeaking. Constrained morphologies, like the channelized one, are particularly sensitive to this change, facing a complete swing in physical habitat dominance in the main channel.

Although impacted by hydropeaking, complex morphologies like the braided and, to a lesser degree, the groynes-controlled, maintain a higher spatial diversity of physical habitats. Notably, for the braided morphology, the area exhibiting low current velocities (physical habitat types 1 and 2) remains relatively constant across the two regimes. However, under hydropeaking, the probabilities of both physical habitat types increase in temporarily inundated shallow areas, potentially introducing a higher risk of drying (Figures 3 and S2). Physical habitat type 1 also changes its location from the main channel to secondary channels under hydropeaking conditions.

In the main channel of the groynes-controlled morphology, physical habitat type 4 dominates,

irrespective of the regime considered. The risk of high current velocity (physical habitat type 5; S2) is higher under hydropeaking. The groyne fields are dominated by physical habitat type 2 in the natural regime and physical habitat types 2 and 3 under hydropeaking. Both physical habitat types are associated with low current velocities, suggesting that groynes-like structures may locally buffer increased current velocities caused by hydropeaking (Ribi et al. 2014). However, drying of shallow physical habitats may be more prevalent in these areas (Figure 3 and S2).

In the alternating bars morphology, physical habitat type 4 prevails in the main channel, while physical habitat type 2 dominates on the bars, regardless of the type of regime. Hydropeaking leads to an expansion in the dominance of physical habitat type 4 and a reduction in physical habitat type 2.

The set of hydro-morphological scenarios exemplify how the metric habitat probability within patches captures the interplay between flow regime and

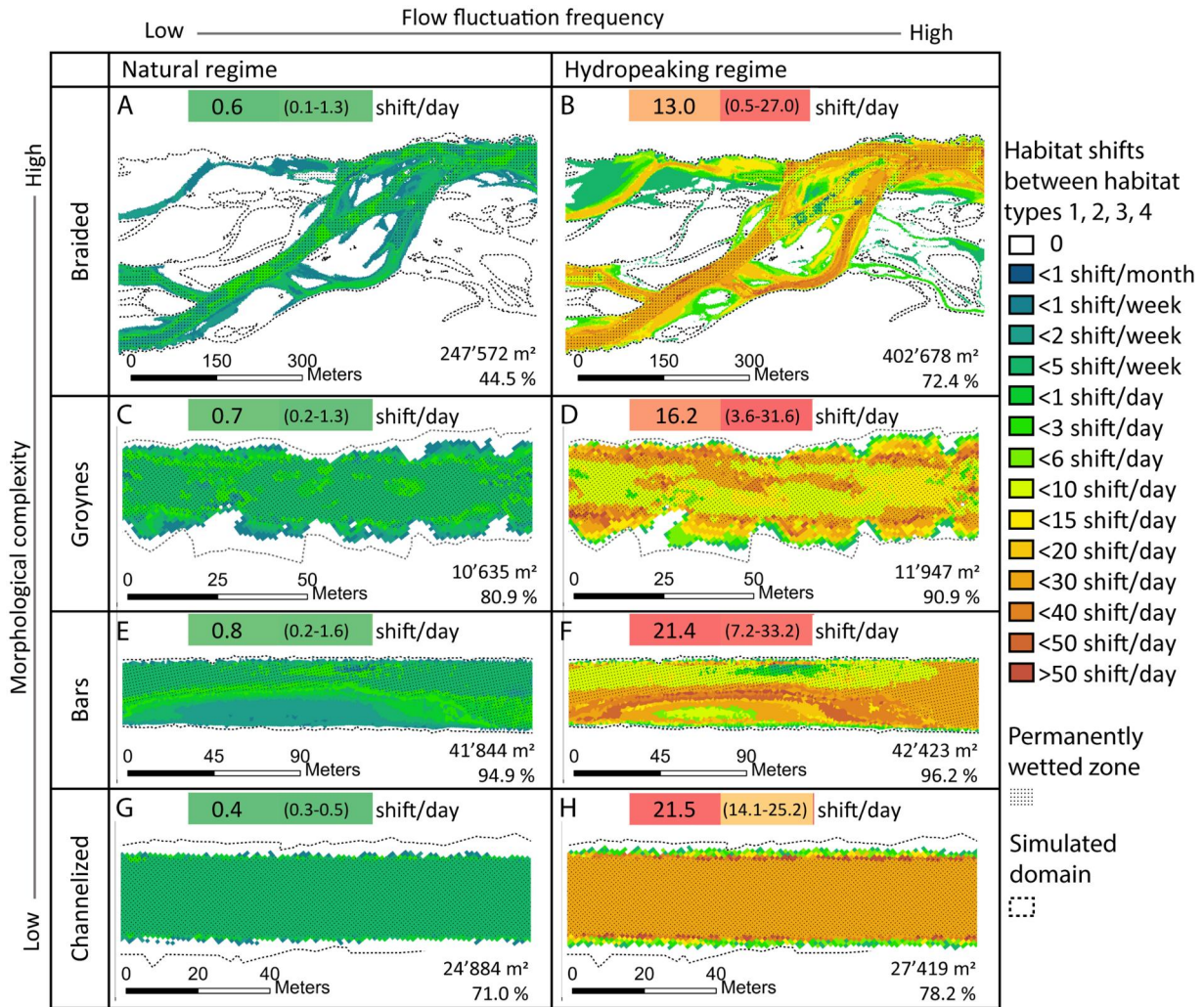


Figure 4. Number of habitat shifts between (physical) habitat types 1, 2, 3 and 4 representing a proxy for the frequency of change in habitat conditions. Shifts to dry conditions and high current velocities are not considered (but see Figures 6 and 7). The number in the centre of each panel indicates the average value for the reach and the background colouring represents the magnitude of the average in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in brackets indicate the 10th and 90th percentile, while the background colouring shows the magnitude of the range between the 10th and 90th percentile in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in the lower right corner of each panel indicate the absolute affected surface and the related percentage of the simulated domain, with the maximum inundated area corresponding to the area inundated at the maximum discharge of 120.0 m³/s. Note the different scales of representation between morphologies.

morphological alterations along different levels of anthropogenic modification. Both flow regime and morphology influence the distribution of habitat types. Open morphologies, such as braided and, to a lesser extent, groynes-controlled morphology, appear to offer increased habitat diversity, potentially enhancing the resilience of river ecosystems towards frequent hydropeaking.

4.2. M2: Habitat shifts within patches

The three types of habitat shifts – shifts between physical habitat types 1 to 4, shifts to dry conditions and shifts to high current velocities – for the eight hydro-morphological scenarios are presented in Figures 4–6. In general, we observe low average values per reach for all three types of shifts

under the natural regime across all four morphologies. However, under hydropeaking, a significant increase of up to two orders of magnitude is observed.

The channelized morphology shows the most substantial increase (54 times higher) in habitat shifts due to hydropeaking, while the braided morphology experiences a 22-fold increase (groynes-controlled experiences 23- and alternating bars 27-fold increase; Figure 4). When examining the spatial distribution, the areas along bars and river margins, as well as in shallow side channels, exhibit the highest number of habitat shifts between physical habitats 1–4 under hydropeaking, regardless of the considered morphology. Compared to the natural regime, habitat shifts under hydropeaking can be locally up to 300 times higher. In comparison,

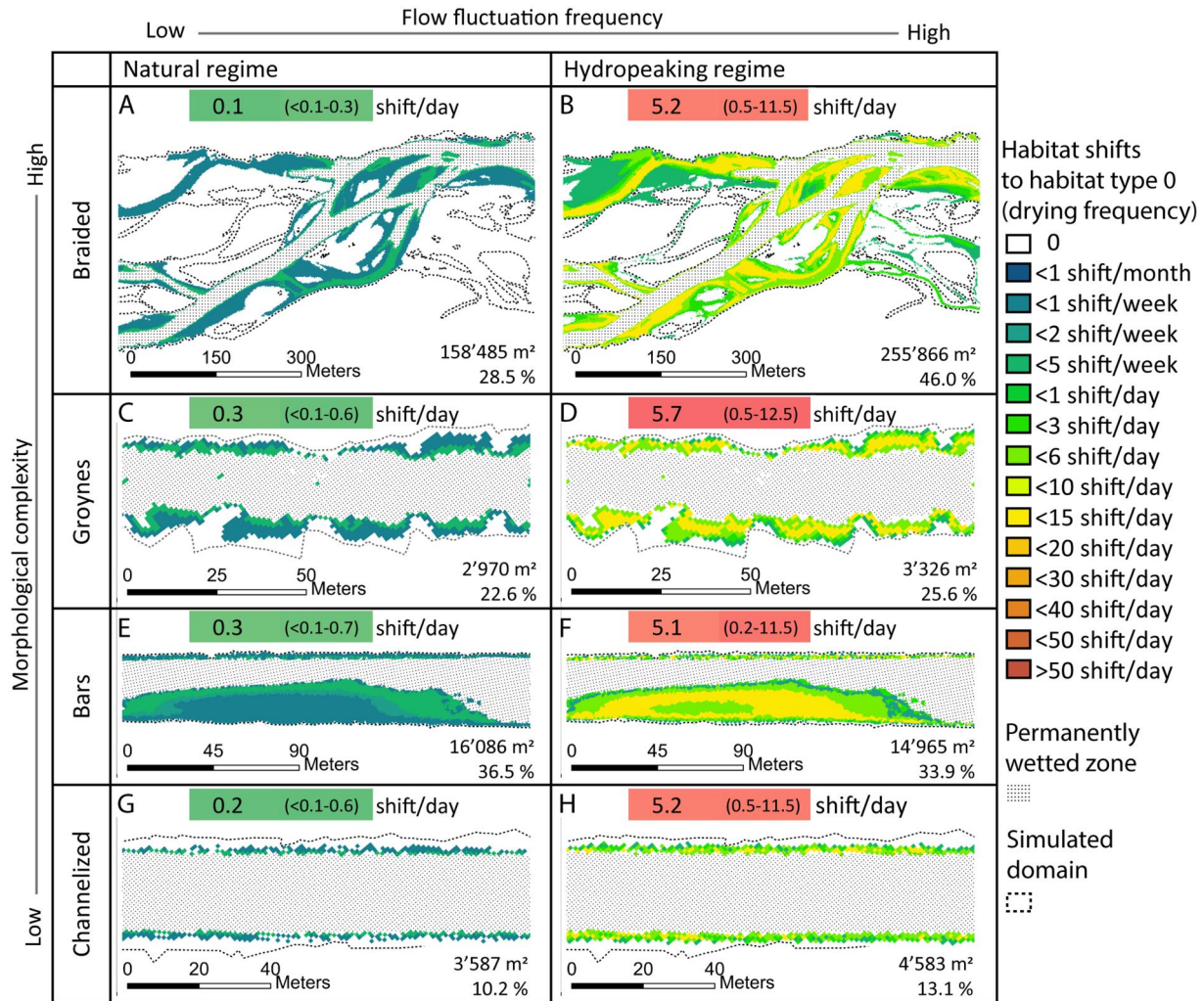


Figure 5. Number of habitat shifts to dry conditions events (i.e. from any physical habitat to type 0) representing a proxy for the frequency of stranding events (i.e. stranding risk). The number in the centre of each panel indicates the average value for the reach and the background colouring represents the magnitude of the average in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in brackets indicate the 10th and 90th percentile, while the background colouring shows the magnitude of the range between the 10th and 90th percentile in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in the lower right corner of each panel indicate the absolute affected surface and the related percentage of the simulated domain, with the maximum inundated area corresponding to the area inundated at the maximum discharge of 120.0 m³/s. Note the different scales of representation between morphologies

habitat shifts in the main channel under hydropeaking are approximately 50–100 times higher than in the natural regime.

On the contrary, the highest increase in habitat shifts to dry conditions, compared to the natural regime, are observed for the braided morphology (52 times higher), followed by channelized (26 times higher), groynes-controlled (19 times higher) and alternating bars morphology (17 times higher; Figure 5). When considering the affected surface, morphologies with a larger dewatering zone are the most heavily affected, as expected. In particular, the braided morphology and, to a lesser extent, groynes-controlled and alternating bars, display large dewatering zones. The channelized morphology only shows a little dewatering zone along the channel margins.

For habitat shifts to high current velocities the most substantial increase is observed in the main channel, with groynes-controlled showing an 18-fold increase, followed by alternating bars (8 times higher) and the channelized morphology (5 times higher; Figure 6). In contrast, the braided morphology exhibits only a small affected area (0.4%) rendering shifts to high current velocities due to hydropeaking negligible.

Comparing the braided morphology with hydropeaking (panels B in Figures 4–6) to the altered morphologies with hydropeaking (panels D, F, H in Figures 4–6), it is evident that morphological alterations only result in minor changes for the three types of considered shifts (ranging between 0.3 and 1.6 times the average of the braided morphology with hydropeaking shown in the panels B). This

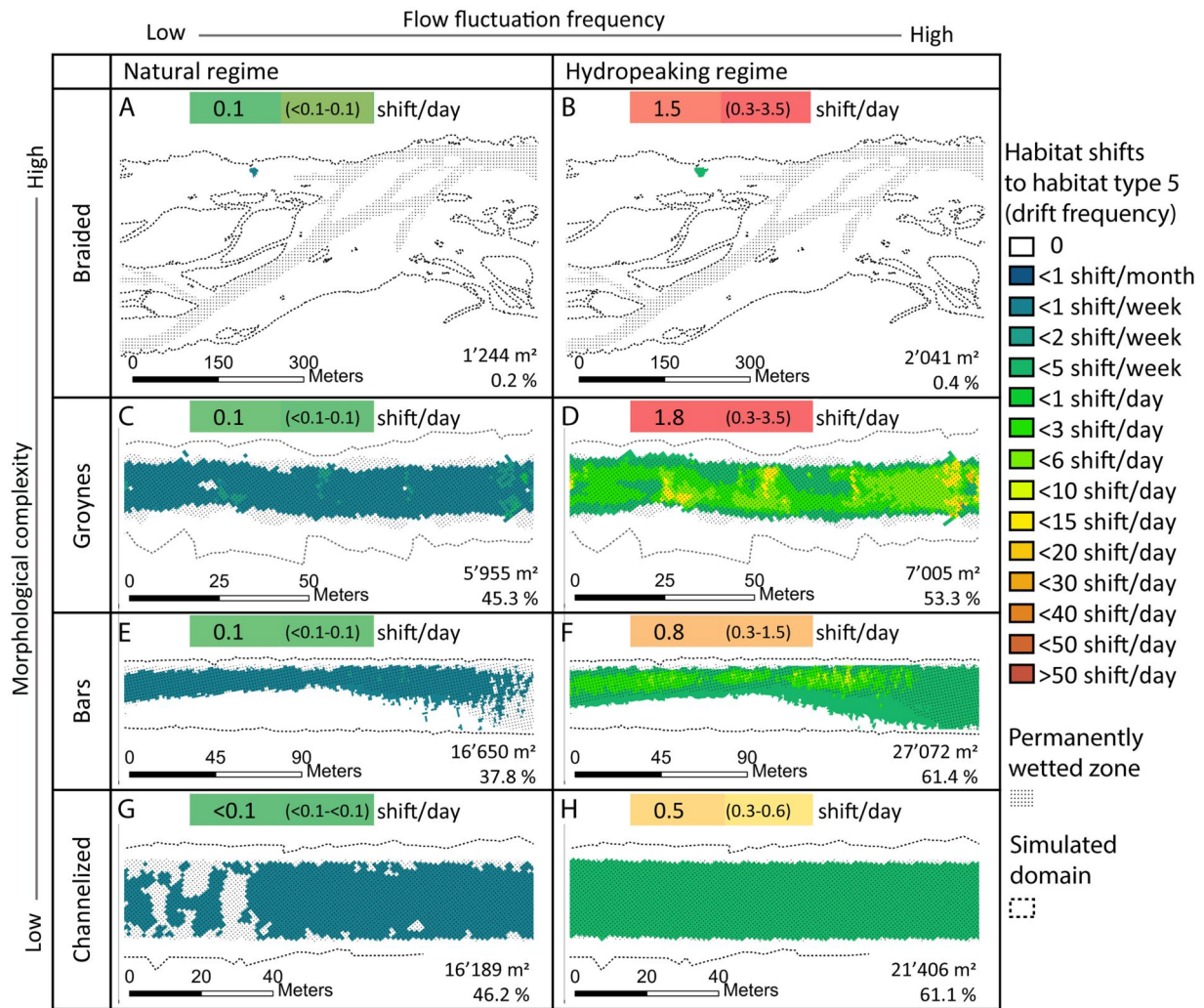


Figure 6. Number of habitat shifts to conditions with high current velocities (i.e. from any physical habitat to type 5) representing a proxy for the frequency of drift events. The number in the centre of each panel indicates the average value for the reach and the background colouring represents the magnitude of the average in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in brackets indicate the 10th and 90th percentile, while the background colouring shows the magnitude of the range between the 10th and 90th percentile in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in the lower right corner of each panel indicate the absolute affected surface and the related percentage of the simulated domain, with the maximum inundated area corresponding to the area inundated at the maximum discharge of 120.0 m³/s. Note the different scales of representation between morphologies.

indicates that, on average, the type of regime has a greater impact on the number of shifts compared to the type of morphology. The overall narrowing of the morphology and the magnitude of flow peaks primarily influence the habitat shifts to high current velocities. In the groynes-controlled, alternating bars and channelized morphologies, large parts of the main channel are affected by high numbers of habitat shifts to high current velocities, whereas the braided morphology only experiences little effects in this regard.

In conclusion, the results from the set of hydro-morphological scenarios suggest that the type of regime has a more pronounced impact on the average number of habitat shifts between physical habitat types 1–4 than the morphology. Hydropeaking, as an altered flow regime, significantly amplifies the number of shifts. Notably, the transition zones between wet and dry conditions, particularly along bars, river

margins and secondary channels, experience the most substantial increases in habitat shifts. Moreover, a reciprocal relationship emerges when examining habitat shifts to dry conditions and habitat shifts to high current velocities. Morphologies that exert a minor influence on one of these type of shifts tend to have a more pronounced effect on the other. This interplay highlights the intricate dynamics between stranding and drift frequencies and underscores the role of river morphology in this relationship.

4.3. M3: Spatial shifts of habitats

Spatial shifts for physical habitat types 1, 2 and 3 were calculated for each hydro-morphological scenario (Figures 7–9). These physical habitat types serve as representative examples of how morphology and regime types can impact habitat characteristics,

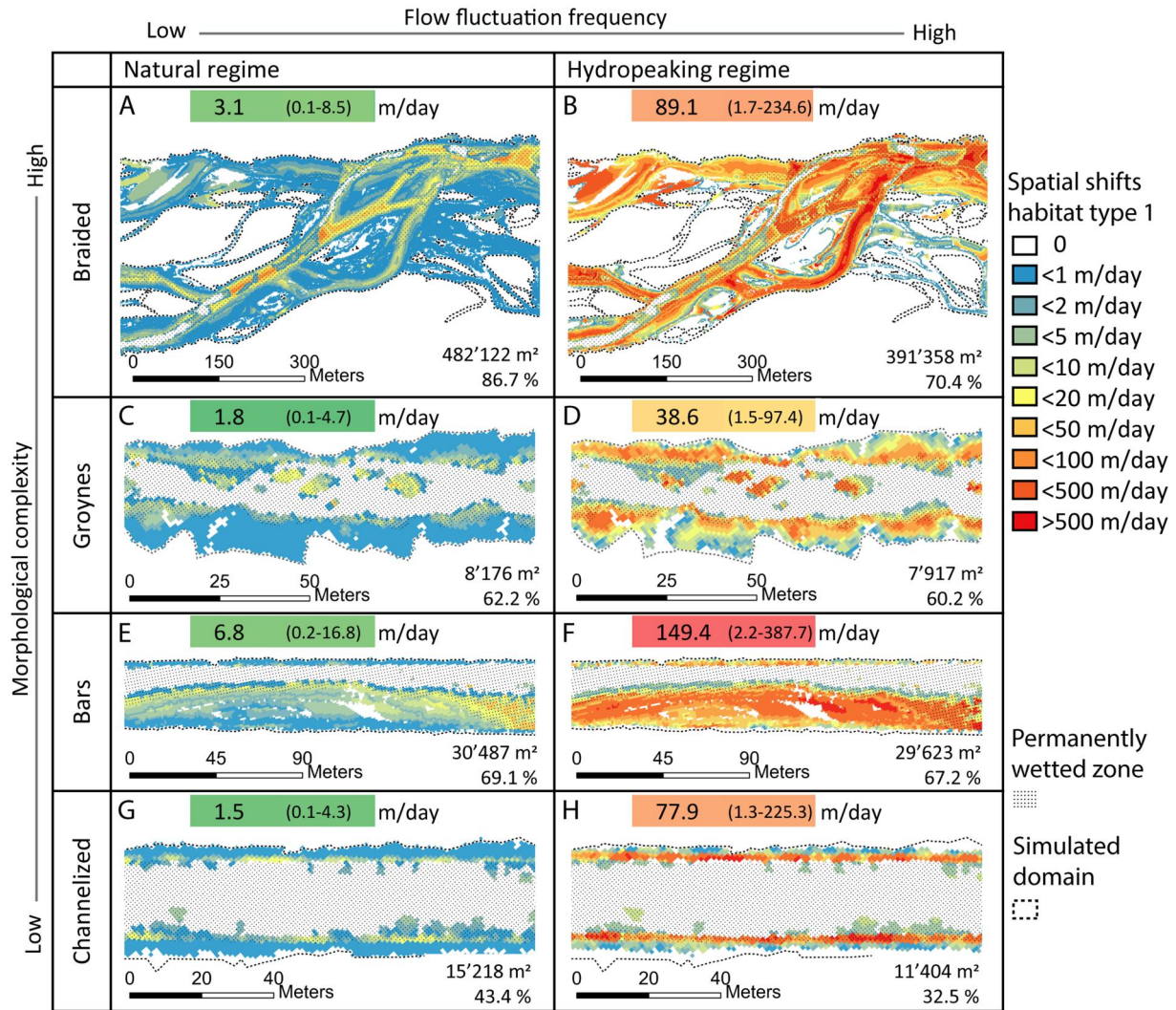


Figure 7. Average spatial shifts (distance) of (physical) habitat type 1. The number in the centre of each panel indicates the average value for the reach and the background colouring represents the magnitude of the average in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in brackets indicate the 10th and 90th percentile, while the background colouring shows the magnitude of the range between the 10th and 90th percentile in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in the lower right corner of each panel indicate the absolute affected surface and the related percentage of the simulated domain, with the maximum inundated area corresponding to the area inundated at the maximum discharge of 120.0 m³/s. Note the different scales of representation between morphologies.

specifically related to shallow water, shallow water with medium current velocity and deep water with low current velocity.

The influence of regime type and morphology varies with respect to the physical habitat type under consideration. Spatial shifts of habitat for all three physical habitat types are generally short under natural regime with average values ranging from 0.4 to 6.8 m/day, depending on the morphology examined. Under the natural regime, the longest average spatial shifts of 6.8 m/day are reached by physical habitat type 3 in the alternating bars morphology.

Under hydropeaking, the channelized morphology exhibits the most pronounced increase in average spatial shifts for physical habitat type 1 and 2, with respective average values being 52 and 75

times higher than in the natural regime. The braided and alternating bars morphologies also demonstrate significant increases (69 and 59 times higher) for physical habitat type 2. Groynes-controlled exhibit the smallest increase for physical habitat type 1 and 2, along with the alternating bars morphology for physical habitat type 1, with values being between 21 and 23 times higher. Nevertheless, the alternating bars morphology shows extensive spatial shifts for physical habitat type 1, with an average of 149.4 m/day and reaching extreme values as high as 387.7 m/day (90th percentile).

Spatial shifts of habitat for physical habitat type 3 exhibit distinct patterns from those of physical habitat type 1 and 2. This is due to the fact that physical habitat type 3 is the least widespread in most hydro-morphological scenarios (Figure 3), resulting

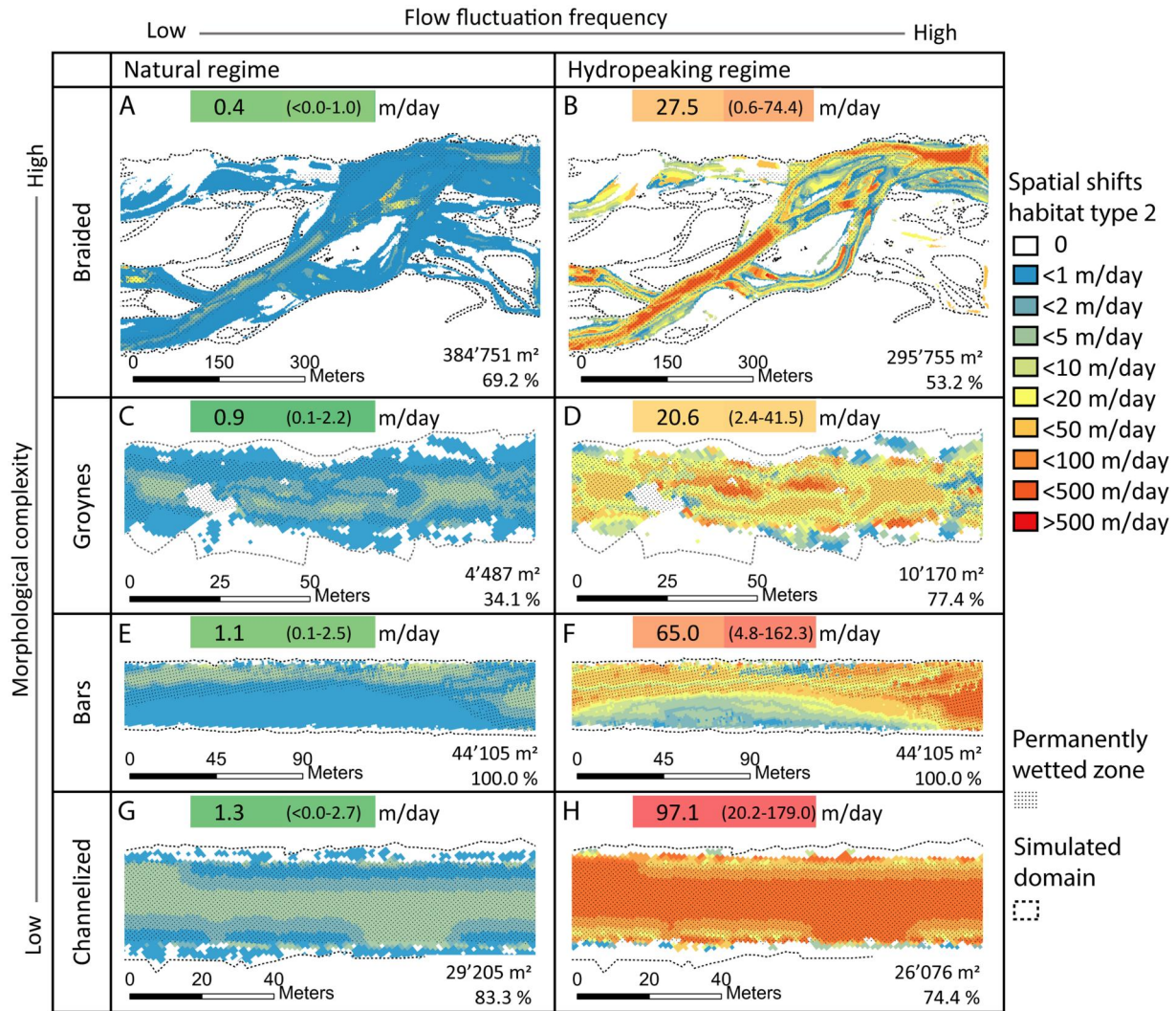


Figure 8. Average spatial shifts (distance) of (physical) habitat type 2. The number in the centre of each panel indicates the average value for the reach and the background colouring represents the magnitude of the average in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in brackets indicate the 10th and 90th percentile, while the background colouring shows the magnitude of the range between the 10th and 90th percentile in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in the lower right corner of each panel indicate the absolute affected surface and the related percentage of the simulated domain, with the maximum inundated area corresponding to the area inundated at the maximum discharge of 120.0 m³/s. Note the different scales of representation between morphologies.

in limited areas displaying spatial shifts (Figure 9). In contrast to physical habitat type 1 and 2, the alternating bars morphology exhibits the highest increase in average values per reach (100 times higher), followed by groynes-controlled (71 times higher). Braided and channelized morphologies also indicate substantial increases (49 and 42 times higher, respectively) compared to the natural regime.

A comparison between the braided morphology with hydropeaking (panel B in Figures 7–9) and the modified morphologies with hydropeaking (panels D, F, H in Figures 7–9) reveals that morphological alterations result in minor changes in the average spatial shifts of habitats for all three considered physical habitat types. These changes range from 0.4

to 3.5 times the average values observed for the braided morphology with hydropeaking.

In summary, the results from the hydro-morphological scenarios suggest that physical habitat types 1 and 2 experience the most significant increases in spatial shifts due to the influence of hydropeaking. However, physical habitat types 1 and 3 exhibit the highest extreme values for spatial shifts. Morphological alterations lead to minor changes in the average spatial shifts. Despite exhibiting higher values of spatial shifts compared to the natural regime, the groynes-controlled morphology consistently shows the lowest values of habitat shifts within patches among all evaluated morphologies under hydropeaking conditions for the specified physical habitat types. These variations in behaviour across

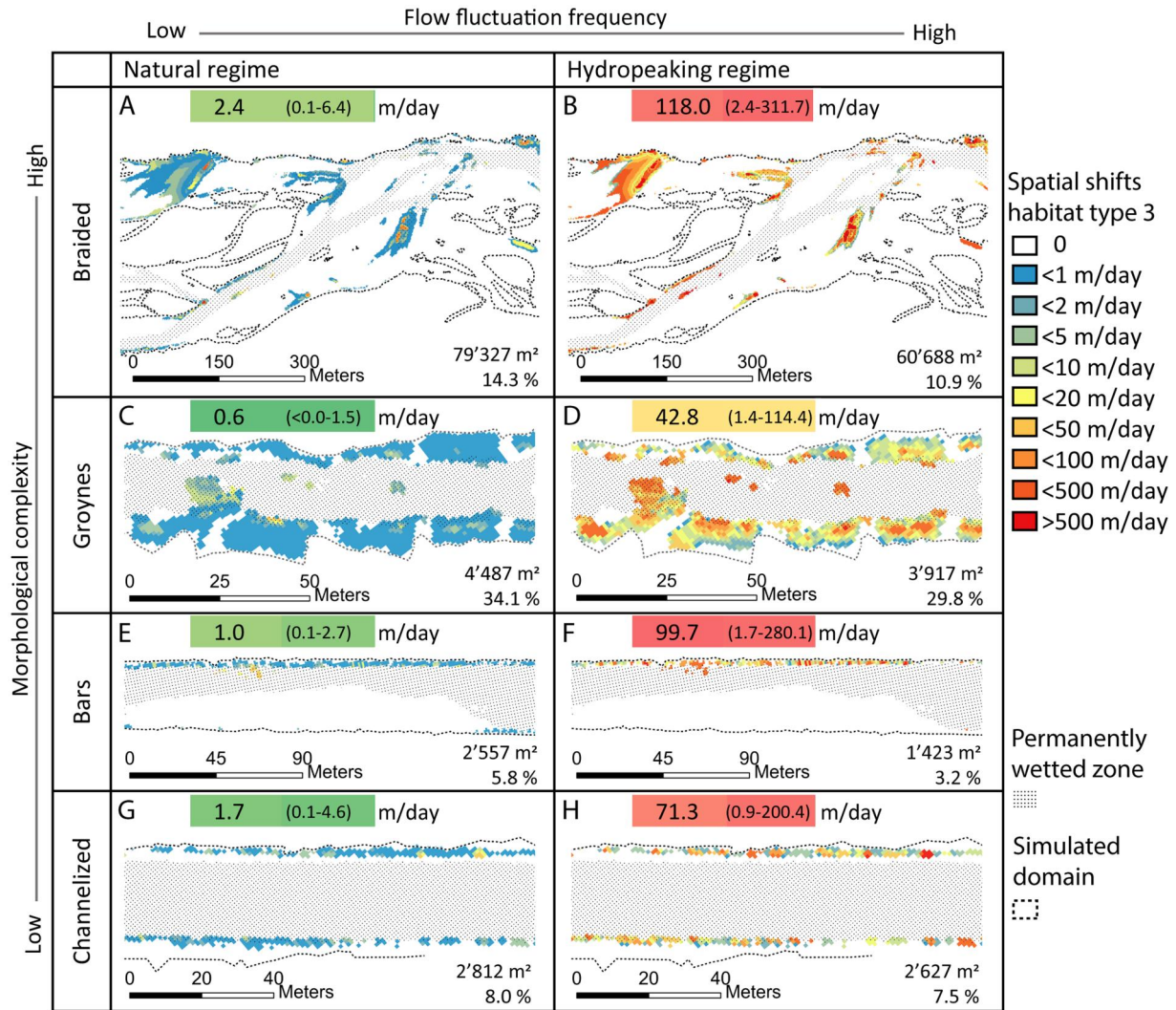


Figure 9. Average spatial shifts (distance) of (physical) habitat type 3. The number in the centre of each panel indicates the average value for the reach and the background colouring represents the magnitude of the average in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in brackets indicate the 10th and 90th percentile, while the background colouring shows the magnitude of the range between the 10th and 90th percentile in comparison to all hydro-morphological scenarios (green = low, red = high). The numbers in the lower right corner of each panel indicate the absolute affected surface and the related percentage of the simulated domain, with the maximum inundated area corresponding to the area inundated at the maximum discharge of 120.0 m³/s. Note the different scales of representation between morphologies.

the considered physical habitat types relate to their spatial distribution within the reach. Spatial shifts for physical habitat type 1 primarily occur within dewatering zones (e.g. bars, secondary channels), while physical habitat type 2 experiences shifts within the permanently wetted zone (e.g. the main channel). Physical habitat type 3 is less prevalent and is dispersed throughout the reach, primarily in areas characterized by deep water with low current velocity (e.g. pools), resulting in extensive spatial shifts.

5. Discussion

In the context of river management and conservation, understanding the effects of different flow regimes and morphologies on habitat dynamics is crucial. Conventional approaches in hydropeaking

mitigation typically rely on hydrological assessments (e.g. Zimmerman et al. 2010; Meile et al. 2011; Bevelhimer et al. 2015; Carolli et al. 2015; Bejarano et al. 2020a; Greimel et al. 2023) and evaluate habitat availability at the reach scale during base and peak flows of a single typical hydropeaking event (e.g. Person 2013; Boavida et al. 2015; Holzapfel et al. 2017; Premstaller et al. 2017; Kopecki et al. 2022; Hauer et al. 2024). Impacts are then assessed based on the total habitat loss between these two flow extremes. Due to their straightforward nature, these methods have found widespread application. However, they often lack the temporal component that captures the cumulative effects of frequent hydropeaking events, which is critical for understanding ecological impacts (Shea and Peterson 2007; Brennan et al. 2019; Bätz et al. 2023),

particularly at the scale of individual habitat patches (e.g. Lancaster and Hildrew 1993a, 1993b; Palmer et al. 2000; Shea and Peterson 2007; McKenzie 2011; Weber et al. 2013; Hitchman et al. 2018; Mathers et al. 2022; Bätz et al. 2023).

More advanced approaches, such as those utilized in this study, rely on habitat time-series to describe habitat dynamics. Habitat duration curves have been used to plot the cumulative frequency or likelihood of a certain amount of habitat at the reach scale (e.g. Weighted Usable Area, WUA) being equaled or exceeded during a specified time period (Bovee 1982; Capra et al. 1995). However, the patch-scale metrics introduced in this study provide a more detailed analysis by allowing for a spatially explicit investigation of how frequent hydropeaking influences the spatio-temporal distribution of hydraulic conditions within individual habitat patches across different morphological settings. By focusing on the patch scale, our metrics reveal the complex interplay between temporal flow variations and morphological complexity, both of which are essential in shaping habitat dynamics and related ecological impacts.

In the following sections, we will first discuss the performance of the patch-scale metrics in representing changes in habitat dynamics at the patch scale due to alterations in flow regime and morphology. We will then explore the ecological relevance of these metrics. Additionally, we will address the limitations of the current patch-scale metrics and explore potential ways to expand them. Finally, we will consider the broader applicability of these metrics to other fields and discuss how to address uncertainties and technical limitations in their use. All aspects are inherently interconnected, with emerging key points for further research from summarised in Table 3

5.1. Performance of the patch-scale metrics

The results from the hydro-morphological scenarios validate the effectiveness of the patch-scale metrics in quantifying the interactive effects of flow regimes and river morphologies on habitat dynamics at the patch scale. The metrics revealed that hydropeaking significantly amplified habitat dynamics, showing an increase of two orders of magnitude compared to the natural regime. While river morphology also influenced habitat dynamics, its impact was less pronounced, causing changes by one order of magnitude. Although different habitat classification methods or mesh resolutions might yield different absolute metric values, the substantial relative differences observed across the various hydro-morphological scenarios give us confidence in the robustness of our findings. Each metric offers a unique perspective on the influence of flow regimes

Table 3. Research needs for understanding the influence of hydropeaking frequency on patch-scale habitat dynamics and ecological responses.

- Establish ecologically meaningful thresholds for the three patch-scale metrics that account for behavioural response (e.g. movement, habitat perception, habitat memory) and associated energy consumption (e.g. for relocation and/or holding position) of selected key species and their life cycle stages.
- Assess the importance of in-stream measures and flow refugia and shelters (e.g. Boavida et al. 2023) in mitigating the effects of increased habitat dynamics caused by hydropeaking to sustain viable populations of riverine organisms (e.g. vegetation, invertebrates, fish).
- Expand the set of patch-scale metrics proposed here by including additional metrics that capture the rate of change and duration between change. Both can be critical for certain processes, such as organism stranding and drift.
- As each patch has its own “habitat persistence regime” (*sensu* Frissell et al. 1986), explore to which extent dynamics of different habitat types change in time (day, season, year, decade) and space (patch, reach, catchment) and how that relates to organisms and their life cycle.
- Investigating the interactive effects among different patch-scale metrics for riverine organism to fully understand the impacts of hydropeaking-induced changes in habitat dynamics (e.g. the impact of stranding risk may depend on the proximity to suitable habitats, the dewatering rate and the frequency of drying).
- Investigating the applicability of the proposed patch-scale metrics for assessing habitat dynamics affected by other flow alterations (e.g. residual flow, climate-change induced modification in flood disturbance) and other types of regime (e.g. sediment transport, water temperature).
- Refining patch-scale metrics involves addressing uncertainties and evaluating their sensitivity within 2D hydrodynamic simulations, particularly concerning the spatio-temporal resolution of input data such as topography, time series, and habitat classifications.

This list builds on the effects of hydropeaking frequency presented in Table 1.

and river morphology on habitat dynamics, providing valuable insights into the complex ecological responses associated with river regulation.

The metric on habitat probability within patches (M1) effectively captures the combined influence of flow regime and morphology on physical habitat distribution and diversity at patch scale over time. Hydropeaking notably alters habitat dominance, especially within the main channel of constrained morphologies like the channelized system, leading to a complete shift in physical habitat types. This drastic change underscores the heightened sensitivity of such morphologies to flow alterations. In contrast, more complex morphologies exhibit greater resilience to hydropeaking, maintaining higher spatial diversity of habitats. For instance, Braided and, to some degree, groynes-controlled morphologies provided greater physical habitat diversity, particularly due to higher probabilities for physical habitats with low current velocities. However, these physical habitats also experienced the most pronounced spatial shifts of habitats (M3) due to hydropeaking. These findings quantitatively supports the notion that complex morphologies can buffer some of the impacts of hydropeaking (Shea and Peterson 2007; Strom et al. 2016; Vanzo et al. 2016), highlighting the importance of considering both flow variability and morphology in habitat assessments (e.g. Lancaster and Hildrew 1993a, 1993b; Palmer et al.

2000; Shea and Peterson 2007; McKenzie 2011; Weber et al. 2013; Strom et al. 2016; Hitchman et al. 2018; Mathers et al. 2022).

The metric on habitat shifts within patches (M2) reveals that hydropeaking significantly increases the frequency of habitat shifts between physical habitat types 1, 2, 3, and 4 compared to natural flow regimes. However, the sensitivity to flow alterations changes with river morphologies, with narrower and less complex morphologies, such as channelized, showing the most pronounced increase in shifts (54 times higher than under natural flow conditions), compared to wider and more complex morphologies like braided systems (22 times higher). The relationship between flow fluctuation frequency and morphological complexity becomes even more apparent when considering the inverse relationship between shifts to drying and shifts to high-current conditions in patches. For instance, drying frequencies due to hydropeaking increase with wider and more complex morphologies, while shifts to high-current conditions are more pronounced in simpler morphologies. This interplay is particularly evident in patches located along bars, river margins, and secondary channels. In line with previous research, wider and more complex morphologies can more effectively redistribute flow pulses, mitigating extreme habitat shifts but this comes at the expense of an increased risk of drying (e.g. Hauer et al. 2014; Vanzo et al. 2016; Auer et al. 2017). This metric therefore allows quantifying the dual role of morphology in either amplifying or mitigating the impacts of hydropeaking on habitat stability and persistence. Both factors are crucial in determining the potential for colonization and survival of organisms in a given patch (Armitage and Pardo 1995; Hitchman et al. 2018; White et al. 2019; Bätz et al. 2023; see also Chapter 5.2).

The metric on spatial shifts of habitats (M3) shows that hydropeaking leads to significant increases in the spatial displacement of the considered physical habitat types. Patches with shallow water and moderate currents, particularly those in transition zones between wet and dry conditions, exhibit the highest spatial displacement. For example, average spatial shifts under hydropeaking can be 59–75 times greater than those observed under natural flow regime. Although morphological complexity has a minor impact on average spatial shifts compared to the type of flow regime (natural or hydropeaking), the groynes-controlled morphology consistently shows lower values of habitat shifts under hydropeaking conditions (between 21 and 23 times higher than natural), suggesting a stabilizing effect on physical habitat displacement. These findings suggest that while increasing

morphological complexity can help buffer some of the impacts of hydropeaking, such as through structural morphological measures (e.g. Bartoň et al. 2023; Friese et al. 2022) or flow shelters (e.g. Ribi et al. 2014; Boavida et al. 2023), it is insufficient to fully mitigate the significant habitat shifts caused by altered flow regimes.

Overall, as demonstrated through the eight hydro-morphological scenarios, the patch-scale metrics developed in this study offer a robust tool for assessing the interactive effects of flow regime and morphology on habitat dynamics at the patch scale. By enabling a more process-oriented understanding of the impacts of flow alterations like hydropeaking, these metrics can better inform river management and support the development of more effective patch specific conservation strategies.

5.2. Ecological relevance of the patch-scale metrics

The ecological relevance of each metric largely depends on the organisms inhabiting specific patches and their mobility (Bätz et al. 2023; Table 1). For instance, habitat shifts within patches (M2) are more critical for less mobile species, such as vegetation and invertebrates, that cannot easily relocate. In contrast, spatial shifts of habitats (M3) are significant for more mobile species, like adult fish, which may need to move frequently to avoid adverse conditions. As discussed in Chapter 5.1, the performance of these metrics effectively captures the interactive effects between the two flow regimes and morphologies. They provide both a generalized understanding of overall habitat dynamics for each hydro-morphological scenario (e.g. through averages) and, due to the patch-scale approach, a spatial assessment of where metric values are highest and lowest. This dual capability not only highlights the practical advantage of these metrics in predicting areas most susceptible to ecological impacts but also allows a better understanding of habitat suitability and stability with respect to organism mobility.

The metrics of habitat probability within patches (M1) and habitat shifts within patches (M2), which were shown to effectively capture habitat persistence and frequency of changes over time in Chapter 5.1, are essential to evaluate habitat quality for organisms with limited mobility, such as vegetation and most macroinvertebrate taxa (Lancaster and Hildrew 1993a, 1993b; Palmer et al. 2000; Bejarano et al. 2018; Mathers et al. 2022). These species are often more vulnerable to changes in habitat conditions, such as drying events caused by hydropeaking. For instance, macroinvertebrate eggs viability is highly sensitive to the drying of shallow habitats

(Kennedy et al. 2016; Miller et al. 2020). Frequent habitat shifts due to recurring hydropeaks (Chapter 5.1) could create critical ecosystem bottlenecks, with cascading effects on other life stages and potentially disrupting the entire food web (Lauters et al. 1996; Bond and Jones 2015; Kennedy et al. 2016; Holzapfel et al. 2017; Miller et al. 2020).

For more mobile species, such as fish, the frequency and magnitude of hydropeaking events can lead to stranding, displacement and increased energy expenditure as they move to find suitable habitats (Nagrodski et al. 2012; Hedger et al. 2018; Hayes et al. submitted). The here proposed metrics tracking habitat shifts within patches (M2) and spatial shifts of habitats (M3) are key for understanding these processes (Chapter 5.1). Rivers experiencing frequent and intense hydropeaking are at risk of degraded fish population structure and community composition, particularly in systems with more than 20 high-flow hydropeaks per year (Schmutz et al. 2015). Fish stranding appears to be one of the main drivers (Hedger et al. 2018; Hayes et al. submitted). However, while here we focus on hydropeaking frequency, hydropeaking magnitude and channel morphology, the impacts on fish population are highly variable between river systems due to the complex interplay of additional patch-scale factors not addressed here, such as substrate type, flow down-ramping rate, peak flow duration, seasonal and daily timing of hydropeaking and water temperature (Berland et al. 2004; Young et al. 2011; Nagrodski et al. 2012; Hauer et al. 2014; Antonetti et al. 2023, Auer et al. 2023; Le Coarer et al. 2023).

Furthermore, recurring hydropeaking often forces mobile organisms such as fish to relocate in search of suitable habitats, with potential implications for their energy budget and overall fitness (Lauters et al. 1996; Lagarrigue et al. 2002; Flodmark et al. 2006; Scruton et al. 2008; Puffer et al. 2015; Rocaspana et al. 2016; Kelly et al. 2017; Puffer et al. 2017). The metric of spatial shifts within habitats is particularly relevant here (Chapter 5.1), as it captures the extent to which habitat types relocate (i.e. shift location) due to repeated flow fluctuations as caused by hydropeaking. Given that swimming energy requirements increase exponentially with current velocity (McKenzie 2011), hydropeaking-induced flow increases can significantly elevate the energy demands for fish, potentially affecting for instance their survival and reproductive success. The observed variability in fish behavioural responses, with some individuals showing high site fidelity (i.e. potential stranding) and others relocating over large distances (i.e. increased energy demand), underscores the importance of considering both habitat shifts within patches (M2) and spatial shifts

of habitats (M3) when understand fish movement behaviour (Kraft 1972; Bunt et al. 1999; Berland et al. 2004; Heggenes et al. 2007; Murchie et al. 2008; Scruton et al. 2008; Boavida et al. 2017; Capra et al. 2017; Lenormand et al. 2021; Cooke et al. 2023).

The ecological relevance of these metrics lies in their ability to capture patch-scale habitat dynamics (as validated in Chapter 5.1), which are essential for effective habitat management (Shea and Peterson 2007). Specifically, they offer a spatially explicit analysis tool for assessing hydropeaking impacts at the patch scale, enabling managers to identify specific action points and implement more targeted and effective habitat management strategies. For example, by pinpointing areas within a river reach that contain the most sensitive habitats (e.g. using habitat probability within patches – M1), managers can develop flow parameters for hydropeaking mitigation that aim to reduce the frequency of habitat shifts within patches (M2) and/or spatial shifts of habitats (M3). This targeted approach not only enhances the ecological resilience of the riverine ecosystem but also optimizes the allocation of resources for conservation and restoration efforts.

5.3. Limitations and expanding the set of patch-scale metrics

While the metrics developed in this study demonstrate ecological relevance by providing valuable insights into habitat dynamics and their potential impacts (Chapter 5.2), one of the primary challenges is establishing ecologically relevant thresholds for the practical application of these patch-scale metrics in management. For instance, the variability in fish response challenges the assumption that fish always select the “optimal” habitats as generally assumed in habitat modelling. Understanding these varied responses of riverine organisms requires considering the complex interplay of factors, such as species-specific life histories, river morphology, hydrology and food availability (Berland et al. 2004; Scruton et al. 2008; Puffer et al. 2015, 2017; Hedger et al. 2023). Behavioural studies, coupled with habitat simulations, can offer deeper insights into how different species interact with their habitats under varying flow regimes. In the absence of precise thresholds, observed natural habitat dynamics may serve as a benchmark, reflecting the conditions to which a specific river ecosystem has adapted and against which the impacts of hydropeaking can be measured (Parasiewicz 2007).

A second challenge arises from the fact that the current patch-scale metrics primarily focus on the frequency of hydropeaking events. However, they do

not capture other critical factors, such as the duration, temporal distribution, and rate of change of these events (Bätz et al. 2023). These factors are essential for understanding the broader ecological impacts of hydropeaking, particularly for species sensitive to changes in flow conditions. For example, increases in current velocity due to hydropeaking can lead to significant habitat shifts, but the rate at which these shifts occur is crucial for predicting the involuntary detachment (i.e. passive drift) of macroinvertebrates within a patch (Brittain and Eikeland 1988; Gibbins et al. 2007; Naman et al. 2016; Schülting et al. 2023; Tonolla et al. 2023). Furthermore, the initial hydropeak typically triggers the most significant macroinvertebrate drift, with subsequent peaks producing less dramatic but still substantial drift responses (Irvine 1985; Irvine and Scott 1988; Bruno et al. 2016). Similarly, fish stranding is influenced by a combination of patch scale factors, including substrate type, flow rates and water temperature, as well as past flow history, peak flow duration and the timing of hydropeaking events (Berland et al. 2004; Young et al. 2011; Nagrodski et al. 2012; Hauer et al. 2014; Le Coarer et al. 2023; Auer et al. 2023; Hayes et al. submitted). This emphasises the need for more patch-scale metrics that capture the various aspects of hydropeaking impact on habitat dynamics and better represent the ecological implications.

Moreover, while developing the patch-scale metrics, we recognized the potential importance of considering the magnitude of shifts between different habitat types. However, the physical habitats used in our study are based on a nominal scale. As a result, we cannot assume that habitat shifts within patches (M2) from one habitat type to another are qualitatively more or less relevant than shifts between other physical habitat types. Similarly, for spatial shifts of habitats (M3), we only considered displacements to the same physical habitat type. However, organisms may also select different habitat types (e.g. refugia; Mathers et al. 2022) during extreme conditions. Incorporating such a concept would require a more species-specific and expert-driven evaluation that allows weighting the observed types of shifts.

These limitations highlight the need for the development of additional patch-scale metrics that can capture a broader range of hydropeaking impacts on habitat dynamics. Future research should aim to address these gaps by creating metrics that consider not only the frequency but also the duration, timing, and sequence of hydropeaking events, thereby providing a more comprehensive understanding of their ecological consequences. Moreover, adapting these metrics to species-specific needs

would enhance the evaluation methods by quantifying the significance of habitat shifts.

5.4. Broader applicability of the patch-scale metrics

Patch-scale metrics offer significant potential for understanding changes in ecological responses over time, yet their full applicability across diverse environmental conditions remains an area of ongoing exploration. One challenge lies in the interactive effects between different metrics, which may themselves fluctuate over time. For example, Lenormand et al. (2021) found that fish typically engage in multiple resting periods each day, cumulatively accounting for half a day without relocation. Seasonal variations also influence fish movement and habitat use in hydropeaking rivers, with generally reduced activity in winter compared to spring and summer (Puffer et al. 2015; Alexandre et al. 2016; Boavida et al. 2017). Disentangling these time-related ecological responses from other influencing factors, such as hydropeaking seasonality, photoperiod, water temperature, and species-specific life strategies, presents a significant challenge (Taylor and Cooke 2012; Puffer et al. 2015; Alexandre et al. 2016; Boavida et al. 2017; Rocaspana et al. 2019). Addressing this complexity would enhance the precision and broader applicability of the proposed metrics.

While this study focuses on the impacts of hydropeaking—an anthropogenic alteration of flow regimes—these patch-scale metrics have the potential to assess a wide range of environmental changes. For instance, rivers subject to residual flows exhibit hydrological characteristics that are opposite to those observed in hydropeaking systems (i.e. very stable versus highly dynamic flows). The same metrics could also be adapted to evaluate the effects of climate change on flow regimes, such as alterations in flood frequency and intensity. Additionally, the metrics could be extended to assess the impacts of other environmental regimes, including temperature fluctuations, sediment transport dynamics and ice formation, which also play crucial roles in determining habitat quality.

Although we refer to these as “metrics” due to their utility in quantifying human impacts on habitat dynamics within a management context, their application extends beyond this scope. These metrics can function as general habitat descriptors, quantifying habitat dynamics as inherent properties of a patch. This perspective allows to move beyond a static view of habitats and acknowledge the dynamic nature of the habitat mosaic (Townsend 1989; Stanford et al. 2005; Shea and Peterson 2007). For

instance, in natural systems, they could help assess the availability and stability of refugia during flood events and understand, how patches affect ecosystem resilience and resistance to disturbance (e.g. Mathers et al. 2022).

Future research should explore the broader applicability of these metrics, particularly in assessing habitat dynamics in both natural and anthropogenically influenced river systems. By expanding the scope of these metrics, we can better understand the diverse ways in which riverine ecosystems respond to environmental changes, ultimately aiding in the development of more effective management strategies.

5.5. Addressing uncertainties and technical limits

Our approach illustrates the great added value of 2D hydrodynamic simulations for understanding the complex interactive effect of flow regime and river morphology on patch dynamics. However, generally, hydrodynamic simulations come with inherent uncertainties and technical limitations. It is important to acknowledge that such simulations may have a high level of local uncertainty regarding hydraulic conditions, particularly for current velocities (Jowett and Duncan 2012; Tonina et al. 2020). Furthermore, 2D hydrodynamics simulation do not capture the 3D hydraulic heterogeneities within each patch, which could however be of importance for many taxa (e.g. flow refugia; Mathers et al. 2022).

Similarly, assessing the sensitivity of the patch-scale metrics in relation to the simulated spatio-temporal resolution is needed. The resolution used in our hydro-morphological scenarios (0.5×0.5 m cells and 10-minute intervals) seems effective in capturing the dynamics of habitat patches.

However, additional analysis is required to further refine the sensitivity and applicability of these metrics. Moreover, the choice of discrete flow values for the simulation could influence the results, as selecting more simulated flows might lead to different patterns of habitat dynamics. In our study, the selection of discharge flows was based on the responsiveness of the four morphologies, particularly in terms of wetted width expansion and flow occurrence frequency. This highlights the importance of carefully considering and adapting the number and range of flows to match specific study objectives and the characteristics of the river being analyzed.

The calculation of these metrics is highly dependent on the availability of accurate, high-resolution data. Flow data must have sufficient temporal resolution to capture rapid changes, especially under hydropeaking conditions, which typically necessitate sub-hourly temporal resolution (Zimmerman et al.

2010; Bevelhimer et al. 2015; Bejarano et al. 2020a). Similarly, high-resolution topographic data (<0.5 m) are essential to accurately represent the changes in hydraulic properties and the associated habitat characteristics at the patch scale (Lepori and Hjerdt 2006; Shea and Peterson 2007; Strom et al. 2016). While we recognize that such detailed data are not always available, many hydropeaking rivers are highly managed, and with the increasing demand for reducing ecological impacts, they often have comprehensive monitoring programs. Thus, while data availability may limit the application of these metrics in some contexts, the method is broadly applicable where adequate monitoring infrastructure exists.

Finally, the analytical treatment of these high-resolution data, especially when analyzing habitat time series at the scale of individual patches over extended periods, requires significant computational effort. This complexity may limit the broader application of the method in settings where advanced computational resources are not available. However, future advancements in computational techniques and increased access to cloud computing, along with the growing availability of high-resolution data, could enhance the applicability of these metrics, enabling their use in a wider range of environments.

6. Conclusions

Hydropower development has significantly altered river flow variability and associated habitat dynamics worldwide (Zarfl et al. 2015; Grill et al. 2019), leading to a significant loss of biodiversity (Lytle and Poff 2004; Ruhi et al. 2018; He et al. 2019; Reid et al. 2019). Hydropeaking, in particular, increases disturbance frequency far beyond natural levels (Archer and Newson 2002; Halleraker et al. 2022; Burman et al. 2023; Greimel et al. 2023). As energy production shifts towards decarbonisation, intermittent power production is increasingly used to balance the intermittency of renewable energies like solar and wind (Kougias et al. 2019; Gonzalez et al. 2023; Koolen et al. 2023), suggesting a rise in hydropeaking frequency in the near future. Consequently, as many ecological impacts are related to hydropeaking frequency (Table 1), habitat evaluation methods must be expanded to account for the effects of hydropeaking's multi-event nature on habitat dynamics (Bätz et al. 2023).

This study introduces three patch-scale metrics designed to quantify temporal variations in habitat within individual patches: (M1) habitat probability within patches, (M2) habitat shifts within patches, and (M3) spatial shifts of habitats. By providing both a generalized (i.e. reach scale) understanding

of habitat dynamics and a spatially explicit analysis, these metrics offer valuable tools for quantifying the ecological impacts of repeated hydropeaking. The metrics demonstrated sensitivity to both flow regime and river morphology, highlighting their utility in identifying areas most susceptible to ecological impacts.

The findings underscore the importance of integrating these metrics into river management to identify spatially explicit and targeted habitat management and restoration. By applying these metrics, river managers can more effectively mitigate the ecological impacts of hydropeaking, promoting the development of functional environmental flows (Hayes et al. 2018; 2019) that not only preserve ecological integrity but also “... permit a positive life history energy balance to sustain a population” (Southwood 1977). Additionally, our approach illustrates the added value of hydrodynamic simulations in understanding the complex interactive effects of flow regime and river morphology on patch dynamics, which is crucial for effectively informing and refining hydropeaking mitigation strategies.

While this study marks a step forward in understanding the ecological impacts of hydropeaking on habitat dynamics, further research is essential to develop additional patch-scale metrics and deepen our understanding of the complex ecological responses in hydropeaking rivers (Table 3). Building on the insights provided here, improving our understanding of the hydropeaking impacts and developing effective management strategies that account for its multi-event nature will enhance our ability to effectively protect and restore river ecosystems.

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Author contributions

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