



Impact of gravel bar flooding on arthropods in the upper Isar: implications for river management

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Abstract. Braided rivers are dynamic ecosystems with constantly shifting flow patterns that create diverse habitats, supporting species highly adapted to frequent flooding and gravel relocation. Arthropods inhabiting these areas use various strategies to survive floods, including migration, hiding, and physiological adaptations like flying or surviving submerged. This study aims to assess whether certain riverbank areas act as refuges during floods and to determine if dominant arthropod species actively or passively respond to rising water levels, with implications for the conservation of these ecosystems. This study focused on the spatial distribution and flood response of two spider species and two beetle species in a gravel bank area along the upper Isar (Germany). Species distributions were recorded under normal conditions and compared to their distribution after a flood event, using 203 sampling squares. In addition, an artificial flood experiment was conducted to observe species behaviour under rising water. Flooding significantly altered the distribution of the studied species, with many individuals relocating to higher areas like slopes during peak flood and scattering across the exposed gravel bar once waters receded. In an artificial flood experiment, individuals initially took refuge in gravel but eventually crossed the water's surface to escape rising water levels, showing varied survival behaviours like floating on stones or paddling to safety. The study highlights the critical role of accessible elevated areas and riverbanks as refuges for arthropods during flooding, with 39% of individuals actively utilizing these sites in response to rising water levels. The findings emphasize that riverbanks and elevated areas must be preserved and managed effectively, as they provide vital refuge conditions for arthropod communities, ultimately fostering ecological resilience in natural river systems.

1 Introduction

Natural braided rivers and their floodplains are highly dynamic ecosystems (Leopold and Wolman, 1957; Tockner et al., 2006; Van der Nat et al., 2003). Their flow patterns, with multiple channels and braids, shift and change constantly over time. This creates a riverbed with varied topography, consisting of an alluvial habitat mosaic that includes all successional stages, from bare gravel to tree-covered patches (Ferguson and Ashworth, 1992; Ward et al., 1999; Ward and Tockner, 2001). Sediment load and flood pulses are the driving forces behind this dynamic (Junk, 1999; Wohl, 2014). The complex flow patterns and the constantly evolving environment are key to the ecosystem's ability to provide habitats for numerous species, most of which are highly adapted to specific conditions. The open, exposed gravel areas form a transitional zone between aquatic and terrestrial habitats. Arthropods inhabiting this zone have evolved various adaptations (Eyre and Lott, 1997; Manderbach, 1998; Framenau et al.,1996; Plachter, 1986) to cope with unpredictable flooding events (Gewässerkundlicher Dienst Bayern, 2025; Campolo et al., 1999). The species living in these harsh environments can employ different strategies to cope with flooding. Some species simply leave the floodplain area during the flood season and resettle during low-flow periods. Resettlement can be either directed or undirected (Rothenbücher and Schaefer, 2006; Weigmann and Wohlgemuth-von Reiche, 1999; Zulka, 1994a). Other strategies to cope with flooding include hiding between the gravel (Andersen, 1968; Kühnelt, 1943; Lehmann, 1965) or escaping to higher elevated areas and trees, which serve as refuge areas (Kühnelt, 1943; Manderbach, 1998; Zulka, 1994a). Physiological adaptations, such as the ability to fly (Andersen, 1968; Bonn, 2000; Desender, 1989; Kühnelt, 1943; Zulka, 1994a) or move on the water surface using surface tension (Kühnelt, 1943; Lambeets and Bonte, 2009; Manderbach and Plachter, 1997; Papi, 1955; Perevozkin et al., 2004; Wessels and Sundermann, 2022), like the two spider genera Arctosa and Pardosa (Kühnelt, 1943), increase the probability of survival. Carabidae and Staphylinidae have been observed to dive and hide under stones using large air pockets beneath their elytra (Kühnelt, 1943; Manderbach and Plachter, 1997). Dorsal ventrally flattened bodies enable Carabidae to hide between gravel (Andersen, 1968; Desender, 1989; Kühnelt, 1943), where air inclusions in unsaturated sediments allow them to survive a flood. Physiological flood resistance and the ability to survive submerged in inundated areas have been described by several authors (Andersen, 1968; Hebets and Chapman, 2000; Kühnelt, 1943; Rothenbücher and Schaefer, 2006; Weigmann and Wohlgemuth-von Reiche, 1999; Zulka, 1994a). Adaptations in life cycles have also been observed (Zulka, 1994b), such as in the spider Arctosa cinerea, which has an asynchronous life cycle, with spiderlings and adults always coexisting. Different habitats for different life stages reduce the loss of a population during flooding. In this regard, larvae of Nebria picicornis were, unlike adults, in areas away from the water's edge (Manderbach and Plachter, 1997). Nevertheless, the majority of the strategies outlined above may prove inadequate when flood events are severe enough to displace entire gravel banks. In such instances, the responses of the species remain largely unknown.

However, understanding how species respond to flood events helps identify key refuges and adaptive strategies, which is essential for conservation efforts as anthropogenic influences such as river regulation, habitat fragmentation, and climate change threaten these natural dynamics, potentially reducing the ability of these systems to support biodiversity. By studying the interactions between species and their environment during flood events, researchers can better inform management strategies aimed at preserving the ecological balance of these systems. Protecting braided rivers not only ensures the survival of the species adapted to these unique habitats but also helps maintain biodiversity on a broader scale, contributing to the resilience of ecosystems and their capacity to provide essential services. In this context, the present study aims to assess, in braided river systems, (1) to which degree riverbanks and elevated areas within the riverbed function as refuges during flood events and (2) to which degree the dominant arthropod species within the studied river section exhibit active or passive responses to rising water levels.

2 Material and methods

2.1 Studied species and study area

This study focused on two spider species, Arctosa cinerea and Pardosa wagleri, as well as the rove beetle Paederidus rubrothoracicus, within the upper Isar between river kilometre 233.8 and 234.1 near Vorderriß (Fig. 1). These three species were identified as the most abundant riparian arthropod species in this area (Wessels and Sundermann, 2022). Additionally, the ground beetle Nebria picicornis and several species of the genus Bembidion were included in the study, as they have been classified by other authors as typical gravel bar inhabitants (Manderbach, 2002). Since specieslevel identification within Bembidion often requires binocular magnification, this genus was recorded collectively without distinguishing individual species. Field studies were conducted in the summer of 2014 on a gravel bank located between the southern riverbank and a primary water channel. The riverbank consists of a steep slope approximately 10 m high. At the ends of the gravel bar, the slope transitions into an almost vertical drop-off edge. The vertical drop-off edge, along with the adjacent forest area, separates the gravel bank from other gravel habitats, making the migration of gravel bank arthropods via this route unlikely. Due to the relatively recent formation of the gravel bank - estimated to be no older than 2 years based on accounts from local residents, aerial photographs from 2012, and structural comparisons with conditions documented in 2011 - vegetation development has not yet commenced.

The study area on the gravel bank was partitioned into sampling squares measuring 5×5 m, resulting in a triangular study site approximately 105 m long and up to 75 m wide (Fig. 2). This configuration encompassed nearly half of the gravel bank. Each square was sampled once per sampling date, with a thorough manual examination conducted for arthropods. Stones were overturned, and finer substrates were sifted using fingers. Larger expanses of fine gravel and sand were carefully raked with a leaf rake. Individuals fleeing from the rake could be quickly spotted on the fine-grained substrate. Although this approach did not constitute a quantitative assessment, the effort for each sampling square was consistent and sufficiently high so that, in our estimation, an even greater effort or a fully quantitative assessment would not have led to fundamentally different results. The individuals of the studied species were counted,



Figure 1. River stretch including the sampled gravel bank (red). Flow direction from left to right.



Figure 2. View from north to the gravel bank, with the study area (framed in red) and the slope in the background.

and their abundance per species within each square was documented. Sampling efforts were conducted on sunny days, ensuring there was no rain or fog, to ensure that many individuals were on the surface. The spatial distribution of the studied species was recorded three times under normal-flow conditions to establish a baseline or a "status-quo scenario". Following a significant flood event, species distribution was recorded again to create a "flood scenario". No surveys were conducted during smaller floods caused by frequent thunderstorms. A single major flood event occurred during the study period. The peak was at the end of July 2014, with a discharge of $152 \text{ m}^3 \text{ s}^{-1}$ (detailed date information is provided in Table 1). A few days after the peak of the flood event, data for the flood scenario were recorded, at a discharge of $37.4 \text{ m}^3 \text{ s}^{-1}$ (Gewässerkundlicher Dienst Bayern, 2025, and Table 1). At this time, the flood had exposed a large part of the gravel bank. An approximately 5 m wide, water-bearing flood channel, a remnant of the floodwaters that had not yet completely receded, separated the slope from the exposed gravel bank. The discharge values in Table 1 should be inter-

preted as guide values. The gauging station is located above the mouth of the Rißbach, and it is not known how much water from the Rißbach was discharged into the Isar during the flood event. The flood altered the dimension of the gravel bar, which made it necessary to adjust the number of sampling squares.

2.2 Response of studied species to an artificial flood

To directly observe the response of the studied species to rising water levels, an artificially induced flood was created. On 25 July 2015, an artificial island composed of sand and gravel, approximately 1 m² in area and about 25 cm in height, was constructed in a side channel approximately 3 m wide. A total of 37 individuals of the studied species were collected from adjacent gravel bars and islands and placed on the artificial island. Following a 1h acclimatization period, the side channel was dammed until the artificial island was completely submerged, which occurred after about 15 min. The reaction of the individuals on the island was observed as the water level rose. Chronological observations were recorded to document whether individuals retreated from the rising water, fled the island, or exhibited other responses, thereby capturing the behavioural repertoire of the species under investigation.

2.3 Statistical analysis

For a visual representation of the studied section of the gravel bar, maps were generated with QGIS version 3.16.13. Due to the constraints imposed by the nature reserve, aerial photos could not be captured on the sampling date due to the breeding season. Instead, maps were created using georeferenced aerial photographs taken the following November, with modifications made to reflect the sampling area and adjacent regions as documented on the sampling day. The data analysis was conducted using R version 4.1.2. In order to compare the data from the different sampling dates, the variance-tomean ratio and the clumping parameter k were calculated for the total number of individuals observed. A variance-to-mean ratio of 1 shows a Poisson distribution, which indicates that the counts are randomly distributed. A variance significantly greater than the mean suggests that the counts are more variable than expected under a Poisson model and may indicate a clumped or aggregated distribution. The clumping parameter k assesses the degree of aggregation within the data, with k < 1 indicating high aggregation and k > 5 indicating randomness (Crawley, 2013). The Wilcoxon test was calculated to compare median values of individual counts of squares adjacent to the main water channel, with those in other squares located on the plateau and slope (Fig. 3), keeping in mind that rank transformation of counts can be unreliable when counts are low.

Unfortunately, the planned continuation of observations in 2015 could not be executed due to the complete erosion of the

gravel bank during the winter. Consequently, further evaluations of the existing data were conducted through qualitative descriptions.

3 Results

3.1 Change in species distribution pattern due to flooding

Altogether, 922 individuals of the studied species were counted across four different sampling dates (Table 1). Of these, *P. wagleri* accounted for 766 individuals, *A. cinerea* for 61 individuals, *P. rubrothoracicus* for 55 individuals, and the beetles for 40 individuals. Four of the beetles belonged to the species *N. picicornis*, while the rest belonged to the genus *Bembidion* sp. Even if there are slight differences between the individual distributions in the status quo before and after the flood, a clear differentiation from the distribution pattern during the flood can be seen (Fig. 4).

3.1.1 Pre-flood

The species distribution pattern (Fig. 5) is very similar for the individuals recorded on both pre-flood sampling dates, with a more frequent occurrence of individuals near the water and a sparser occurrence on the plateau. On both sampling dates, the number of individuals per square along the main water channel was significantly higher than in squares not adjacent to the water's edge (Wilcoxon rank-sum test p = 0.000-0.027). None of the examined species were found on the riverbank or the slope.

3.1.2 Flood scenario

A different distribution pattern emerged during a flood. Of the individuals, 38.8 % were found on the slope, with an average of 3.8 individuals per sampling square (Table 2). Both spider species and the rove beetle were present (Table 3), but no ground beetles were found. The remaining individuals were scattered across the gravel bar, with an average of 1.3 individuals per sampling square. Two larger clusters were found around deadwood and smaller organic debris washed ashore. The Wilcoxon rank-sum test found no significant difference between the number of individuals found in squares next to the main water channel and those in the other squares on the plateau, riverbank, and slope (p = 0.958).

3.1.3 Post-flood

The distribution of individuals was again oriented towards the water's edge. On the plateau, some clusters of individuals were found on sampling squares with accumulations of organic matter. The differences between the number of individuals found in sampling squares next to the main water channel and those in other squares on the plateau and slope were not significant (p = 0.027) (compare also Fig. 5). **Table 1.** Number of individuals per sampling date and discharge scenario. Results are given for the variance-to-mean ratio, the clumping parameter k, and the Wilcoxon test.

		Status-quo scenario: 4 July 2014	Status-quo scenario: 16 July 2014	Flood scenario: 4 August 2014	Status-quo scenario: 19 September 2014
Discharge [m ³ s ⁻¹]		6.28	4.11	37.4	5.58
Individuals		249	324	98	251
Variance to mean		12.78	8.29	4.63	13.46
k		0.1	0.22	0.49	0.1
Significant difference between individual numbers		yes $(p = 0.000)$	yes $(p = 0.000)$	no ($p = 0.958$)	no $(p = 0.027)$
per sampling square along the water's edge and					
per square on the slope and plateau					
Sampling squares (all examined)		203	203	55	208
Sampling squares (all examined and flooded)		203	203	80	208
Sampling squares (occupied ones)		51	95	24	34
Total number of indi	viduals per species				
A. cinerea	Total	25	25	4	7
	Adult	19	11	1	5
	Spiderling	6	14	3	2
P. wagleri	Total	193	254	81	238
	Adult	146	98	19	136
	Cocoon	15	15	1	0
	Spiderling	32	141	61	102
P. rubrothoracicus		18	30	5	2
N. picicornis		2	0	2	0
Bembidion sp.		11	15	6	4



Figure 3. Location and classification of the sampling squares adjacent to the main water channel (beige) and those located on the plateau (light brown) and at the slope (dark brown) for the status-quo (July) and flood scenario (August), with the number of sampling squares in brackets.

3.2 Response of the studied species to flooding

The individuals (Table 4) released on the artificial island quickly spread out and hid in the gravel. When they came to the surface of the water, they returned to the artificial island, drifted, or continued toward the opposite side of the water. When the rising water level drove the animals from their hiding places, this behaviour was repeated. As the area of the artificial island shrank, the animals increasingly ventured onto the water's surface. Shortly before the island was completely flooded, the animals no longer avoided the approaching waterline but ran directly across the water's surface to the opposite gravel bar upon contact with the water. In the end, only two *P. wagleri* individuals remained and moved across the water's surface toward a nearby gravel bar.

The *Bembidion* individuals also dodged the approaching waterline until the area became too small for them to retreat, at which point they paddled to a nearby gravel bar. One *Bembidion* had retreated to an elevated stone. When the rising water reached the *Bembidion*, it attempted to fly but failed. The two individuals of *N*. *picicornis* had already left the artificial island when the substrate became damp due to the





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Figure 5. Distribution of the studied species on different sampling dates. On 4 August 2014, data were collected 4d after a flood that completely submerged the gravel bar. The extent of the gravel bank shown corresponds to the water level at the time of data collection.

rising water. They ran across the surface of the water to a nearby gravel bank.

4 Discussion

To better understand the habitat requirement of the arthropod community on gravel bars, we examined the importance of elevated areas and riverbanks during flooding. The results indicate that elevated areas in the riverbed and riverbanks serve as refuge sites, actively visited by 39 % of the total number of collected individuals during a flood. Our study demonstrated that retreating to higher ground was a dominant response compared to fleeing across the water onto other gravel bars in reaction to rising water levels. Notably, the animals that retreated to the slope occupied a habitat they would typically have avoided, as noted by Wessels and Sundermann (2022), in the absence of flooding.

Some individuals might not have avoided the flood and instead survived in the inundated interstitial spaces, as evidenced by a single *Bembidion* specimen observed during this study, which is also supported by existing literature (Andersen, 1968; Manderbach, 1998; Kühnelt, 1943; Zulka, 1994a). It remains unclear whether the other individuals found on the plateau survived flooding in the interstitial spaces, migrated from the slope over the small water channel, or were washed up by rising water. Other described but unobserved behaviours of the species examined include diving to hide in the underwater interstitial, drifting on the water surface, and – for Carabidae – escaping through the air. However, it is unclear which criteria the animals use to determine their strategy in response to flooding.

4.1 Status-quo distribution

Gravel-bank-dwelling arthropods are typically found along the water's edge, a behaviour closely linked to food availability. Depending on the season, the primary food source for these arthropods consists of aquatic insects, which either drift from the water or emerge as adults (Briers et al., 2005; Hering and Plachter, 1997; Langhans and Tockner, 2014). During hatching events, the abundance of these insects creates a concentrated and readily accessible food supply along the water's edge. Consequently, arthropods are more likely to

	Water	Plateau	Slope	Sum
4 July 2014				
Squares	39	143	21	203
Individuals	192	57	0	249
Individuals per square	4.92	0.40	0.00	1.23
Percent of individuals	77.1	22.9	0.0	
16 July 2014				
Squares	39	143	21	203
Individuals	218	106	0	324
Individuals per square	5.59	0.74	0.00	1.60
Percent of individuals	67.3	32.7	0.0	
4 August 2014				
Squares	15	30	10	55
Individuals	18	42	38	98
Individuals per square	1.20	1.40	3.80	1.78
Percent of individuals	18.4	42.9	38.8	
19 September 2014				
Squares	54	131	23	208
Individuals	89	162	0	251
Individuals per square	1.65	1.24	0.00	1.21
Percent of individuals	35.5	64.5	0.0	

Table 2. Number of individuals per sampling date and square.

 Table 3. Number of individuals per species recorded during the flood scenario.

		Water	Plateau	Slope
A. cinerea	Adult	0	1	0
	Spiderling	0	1	2
P. wagleri	Adult	3	3	14
	Spiderling	11	31	19
P. rubrotho	racicus	1	1	3
N. picicorn	is	1	1	0
Bembidion sp.		2	4	0

stay near the water's edge, where they can capitalize on this resource.

4.2 Flood-response-triggering factors

One criterion that may influence the nature of the response to floods is the current phase of the life cycle. For instance, the wolf spider *Tricca lutetiana* was observed to remain in its burrow at all times while it had a cocoon, without leaving under any circumstances that might lead to flooding (Dolejš et al., 2010). A similar situation was noted for a single female *A. cinerea* with a cocoon, which was located in an elevated, vegetated, and heavily silted area with a comparatively high abundance of ants, inside a burrow beneath a stone, with the entrance sealed by woven silk (Wessels and Sundermann, **Table 4.** Number of individuals used in the behavioural experiment on rising water levels.

	Total number	First experiment	Second experiment
Total number	37	19	18
A. cinerea	-	_	_
P. wagleri	16	9	7
P. rubrothoracicus	15	8	7
N. picicornis	2	_	2
Bembidion sp.	4	2	2

2022). A female *Arctosa maculata* carrying a cocoon was also observed sitting in its submerged burrow, awaiting the end of the flood (Wessels and Sundermann, 2022). However, further literature on the wolf spider *A. cinerea* staying in its burrow during a flood does not provide information regarding the life phase of the individuals affected or whether they possessed a cocoon (Bellmann, 2010; Panait, 2005).

The nature of the response to floods can also be influenced by the current location of the affected individuals. For example, burrowed larvae of various *Bembidion* and Staphylinidae species survived flooding in the interstitial spaces, while individuals on the surface were carried away by the current (Andersen, 1968).

Another criterion that may determine the strategy employed is weather conditions. *Bembidion* individuals have been observed to fly from the water surface (Andersen, 1968), even at temperatures of around 16 °C during floods (Zulka, 1994a); however, they were unable to fly during winter (Manderbach, 1998) or on cool late-spring days with temperatures of around 10 °C (Wessels, unpublished data, 2014/15). On warm and sunny days, collecting individuals of the genus *Bembidion* proved challenging because they would fly away (unpublished data, 2014/15). This, along with the observation of a single *Bembidion* specimen that was unable to take off in the present study despite temperatures of around 22 °C, suggests that the ability to fly cannot be generalized across all individuals.

Temperature and light intensity significantly influenced the movement patterns of the studied *Bembidion* species. Individuals oriented toward the light at warm temperatures (15 °C and above) and toward dark silhouettes during colder temperatures (6 °C and below). This behaviour was independent of the experimental design (Andersen, 2006). This photosensitive reaction may explain behaviours such as the significantly decreased tendency of drifting individuals of the wolf spider *Pardosa agricola* to move ashore under sunny weather conditions (Lambeets et al., 2010). Similarly, individuals of *P. wagleri* were observed on warm summer days during data collection for the present study and other studies (Wessels and Sundermann, 2022), as they fled startled onto the water and remained some distance from the gravel bank, partially drifting away with the current. Overall, this response can lead to a migration to elevated areas during rainy weather to avoid a subsequent flooding. Conversely, on sunny days, such as the day the present study was conducted, this response increases the risk of individuals drifting, which may facilitate the recolonization of new gravel bars.

4.3 Population collapse and recovery induced by flooding

The literature describes that flooding leads to a collapse in surveyed arthropod populations (Hering et al., 2004; Manderbach and Plachter, 1997; Manderbach, 2001; Vanbergen et al., 2017). This phenomenon was also observed in our study, as fewer individuals were recorded following the flood. A detailed analysis of the carabid abundance at species level by Vanbergen et al. (2017) revealed that only wingless species were negatively affected by flooding. Due to high reproduction rates and strong dispersal abilities, the riparian arthropod communities typically recover within the same year (Bates et al., 2006; Hering et al., 2004; Kühnelt, 1943; Manderbach and Plachter, 1997; Manderbach, 2001). However, 1 month after the flood event, the number of individuals per square in our study approached the numbers before the flood event. However, it is unclear whether and, if so, what role animals that survived the flood in the interstitial played. Floods contribute to population recovery by resetting the successional stages (Larsen et al., 2019; Plachter, 1998), which helps preserve the system and provides a habitat for the gravel bar arthropod community. Additionally, flooding washes aquatic food onto riverine sediments (O'Callaghan et al., 2013; Tockner and Waringer, 1997). As a result, Hering et al. (2004) reported an increase in ground beetle species following a major flood. In the present study, the distribution of individuals across the sampling area on 19 September 2014 may indicate such an enrichment of food. Driftwood and organic matter washed ashore are known to harbour displaced arthropods (Tenzer, 2003; Zulka, 1994a), which may explain the clustering of individuals of the studied species that prey upon them.

4.4 Riverbanks and elevated areas as refuges during flooding

With more than 80% of the riverbed being relocated during a single flood event (Van der Nat et al., 2003), the role of elevated areas within the riverbed and riverbanks in population recovery and resettlement is likely significant and should not be underestimated. The results of the present study, where 39% of the total number of individuals were found on the riverbank during a flood, support this assumption. Indeed, elevated areas and riverbanks accessible to the riparian arthropods have been identified as important variables in several studies (Bell et al., 1999; Wessels and Sundermann, 2022). Abundance and, in some cases, species richness were the highest near elevated areas and riverbanks (Lambeets et al., 2009; Wessels and Sundermann, 2022), a trend that was also observed in organisms inhabiting interstitial spaces at a depth of 50 cm (Marmonier et al., 2019).

Although specific conditions required for riverbanks to function as flood refuges are not explicitly documented in the literature, it is likely that the stenotopic species of open gravel banks require conditions similar to those of their typical habitats. For example, the spider species *A. cinerea* and *P. wagleri* avoid areas with more than sparse vegetation (Framenau et al., 1996; Schatz et al., 2003; Wessels and Sundermann, 2022), possibly due to increased competition from generalist species or predators. Formicidae, with their efficient and aggressive foraging behaviour, are strong competitors, often outcompeting other arthropods for resources. Their dominance is further reinforced by their role as predators, as they directly hunt other gravel bank inhabitants, including arthropods (Hering, 1995; Wessels and Sundermann, 2022).

Riverbanks with these characteristics are found in seminatural or natural river systems with lateral channel migration. In these systems, riverbanks, like the riverbed, are subject to regular erosion and deposition, creating the necessary refuges. This watercourse management should consider not only the riverbed but also the riverbanks and adjacent areas. This conclusion aligns with the recommendations of other authors (Rothenbücher and Schaefer, 2006; Ward et al., 2001) to protect species by safeguarding ecological processes at the landscape level.

Code and data availability. All data used in this study are available in the Supplement, which provides code and the complete dataset supporting the results and conclusions of this article.

Supplement. The supplement related to this article is available online at https://doi.org/10.5194/we-25-91-2025-supplement.

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