



Stream connectivity and governing processes in high-mountain wetlands

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15 **Abstract.** High-mountain wetlands (*hereafter* wetlands) have the potential to store and release large volumes of water. They provide substantial contributions to water supply for highland communities and receiving lowlands and their extended residence times can buffer water demand during drier periods. Despite their hydrological significance, major gaps remain in understanding the connection between wetlands and streams, which prevents us from accurately conceptualising them in models. We used a combination of conservative fluorescent tracing and monitoring of rainfall-runoff and wetland water

20 levels to develop a perceptual model of connectivity between wetlands and streams. The experiments were conducted during the wet or dry season in five study catchments (0.38 km² – 12.58 km²) from northern Ecuador to southern Peru. Fluorescein was introduced into wetlands and monitored downstream with activated carbon samplers for 5-12 months. Our results suggest travel times from less than 1 week to upwards of 3 ½ months, with one experiment seeing little to no response. Results indicate that wetlands have a stronger hydrological connection to streams in the wet season than in the dry season,

25 where in some cases we observed no connection at all. Multiple peaks in fluorescein concentration from a single injection during the wet season may suggest that the wetlands contribute to streamflow via multiple pathways and processes. The results demonstrate a complex connection between wetlands and streams, controlled by topographic configuration and season, amongst other factors. However, persistent contributions from wetlands to streams observed several months after dye introduction support their significance to downstream, year-round water supply. The results provide improved understanding

30 of wetland-stream connectivity that informs the development of models to address the need for site-specific evidence of wetlands' influence on water supply and the ability to scale this information in space and time.



1 Introduction

High-mountain wetlands (*hereafter* wetlands) may cover an estimated area of over 30,500 km² in the world's major mountain regions (Becker et al., 2026) and provide essential water storage, provision and regulation services (e.g., Millennium Ecosystem Assessment, 2005; Chatterjee et al., 2010; Gandarillas R., Jiang and Irvine, 2016; Lazo et al., 2019; Ross et al., 2023). These services may be critical in seasonally dry climates and mountain regions highly vulnerable to water insecurity, such as the tropical Andes and high-mountain Asia (Immerzeel et al., 2020) but are under severe threat from climate (Xue et al., 2014; Otto and Gibbons, 2017) and land use and land cover changes (e.g., Maldonado Fonkén, 2014; Ochoa-Tocachi et al., 2016; Guo et al., 2020; Ross et al., 2026). Policy and decision-making concerning the conservation and restoration of wetlands require solid evidence of their hydrological connectivity to streams to understand their influence on basin-wide water supply (Golden et al., 2014). Several localised studies have successfully demonstrated the critical role of wetlands at the headwater scale (e.g., Ross et al., 2023; Wunderlich et al., 2023; Gribbin et al., 2024). However, to improve relevance at the regional, national and international level, local-scale hydrological knowledge must be combined with modelling (Golden et al., 2017; Jones et al., 2019). A common approach incorporates 'wetland module(s)' into a process-based hydrological model (e.g., Evenson et al., 2015, 2016, 2018; Fossey and Rousseau, 2016; Fossey et al., 2016; Lee et al., 2018; Muhammad et al., 2019; Wu et al., 2020). This requires a hydrological conceptualisation of wetlands, including their connectivity to the wider catchment and each other. The behaviour of wetlands, however, cannot be easily generalised – even similar seeming wetlands may be driven by different processes (Bullock and Acreman, 2003). Many factors control divergent wetland behaviour, such as topography, soil characteristics and position in the landscape (Acreman and Holden, 2013; Åhlén et al., 2022), including whether they are riparian or embedded (Fossey et al., 2016; Wu et al., 2020). Wetlands may also have temporal variations in hydrological behaviour and connectivity (Evenson et al., 2018), notably in regions with high seasonality (Ross et al., 2023).

A major knowledge gap when assessing the contribution of wetlands to water supply is an accurate representation of their connectivity (Golden et al., 2014, 2017), including spatial and temporal controls on their connectivity and subsequent transit times (Soulsby et al., 2015; Correa et al., 2017). Wetland connectivity is defined as the transfer of water between wetlands and their surrounding watershed components (Jones et al., 2019). Studies often use naturally occurring tracers, such as stable isotopes (e.g., Lyon et al., 2010; Tetzlaff et al., 2014; Birkel et al., 2015; Soulsby et al., 2015; Lazo et al., 2019; Mosquera et al., 2016b), chloride [Cl⁻] (e.g., Hrachowitz et al., 2010, 2009a, 2009b; Thorslund et al., 2018; Leach et al., 2020), electrical conductivity (e.g., Ali et al., 2017; Mosquera et al., 2018; Lazo et al., 2023, 2024; Mosquera et al., 2016b) or dissolved organic carbon (DOC, Pesántez et al., 2023a, 2023b), to assess connectivity and estimate transit times in wetland dominated catchments. These often give a lumped catchment estimate of transit time, assuming linearity (steady-state conditions) and not accounting explicitly for wetland influence. A conceptual model can be coupled with a tracer mixing model (e.g., Birkel et al., 2015; Pesántez et al., 2023a) which may be used to simulate wetland residence times and contributions to streamflow



more explicitly. Additionally, transit times across several catchments can be statistically related to wetland coverage (e.g., Lyon et al., 2010; Mosquera et al., 2016b), which, when combined with other catchment characteristics, may allow us to predict the influence of wetland coverage on transit times in ungauged basins (Tetzlaff et al., 2009, 2010; Hrachowitz et al., 2009a). Tracers can also provide insights into the mechanisms by which different sources feed streamflow (e.g., Berghuijs and Kirchner, 2017; Sprenger et al., 2019). More intensive methods analyse stable isotopes of water samples from specific depths in the soil profile to directly estimate wetland residence times and storage (e.g., Tetzlaff et al., 2014; Lazo et al., 2019). However, recent approaches have shown potential for quantifying multiple sources using only a single tracer (e.g., Kirchner, 2023).

Tracer-based studies into the transit times and connectivity of natural wetlands have been limited to northern sites in Scandinavia (e.g., Lyon et al., 2010), North America (e.g., Ali et al., 2017; Brooks et al., 2018; Thorslund et al., 2018; Lane et al., 2020; Leach et al., 2020) and Scotland (e.g., Tetzlaff et al., 2014; Birkel et al., 2015; Soulsby et al., 2015), in addition to increasing studies from the Zhurucay experimental catchment in Ecuador (e.g., Correa et al., 2017; Lazo et al., 2019; Mosquera et al., 2016b). Few of these studies have conducted comparable experiments in multiple catchments to explore and compare the controls on wetland connectivity and transit times. Existing studies show a strong geographical bias towards temperate and cold regions, with very few studies in tropical and subtropical mountain regions. Their complex topographic configurations combined with the strong and diverse climate seasonality requires further investigation, through field-based experiments and monitoring (Acreman and Miller, 2007; Burt and McDonnell, 2015), into the connectivity of wetlands in these ecosystems.

Robust, easily reproducible methods are needed to assess connectivity mechanisms across several sites and quantify their physical and climatic controls, to scale them in space and time. Fluorescent tracing analysis has successfully demonstrated connectivity and constrained travel times in Andean nature-based systems, including drainage canals known locally as “amunas” and irrigation ditches in Peru and Ecuador (Ochoa-Tocachi et al., 2019; Matovelle et al., 2025). Here, we combine conservative fluorescent tracer dye experiments with hydrometric monitoring to assess connectivity mechanisms and their controls across five high-altitude catchments from Northern Ecuador to Southern Peru in both wet and dry seasons. We use this analysis to (1) get a direct estimate of travel times between wetlands and streams, (2) evaluate the physical and climatic controls on wetland-stream connectivity and travel times and (3) develop a perceptual model that captures wetland-stream connectivity mechanisms and their controls to inform future modelling approaches. Our analysis allows for direct insights into wetland-stream connectivity and provides a methodology that can be implemented easily across a large network of catchments to further our understanding of these mechanisms and their governing processes.



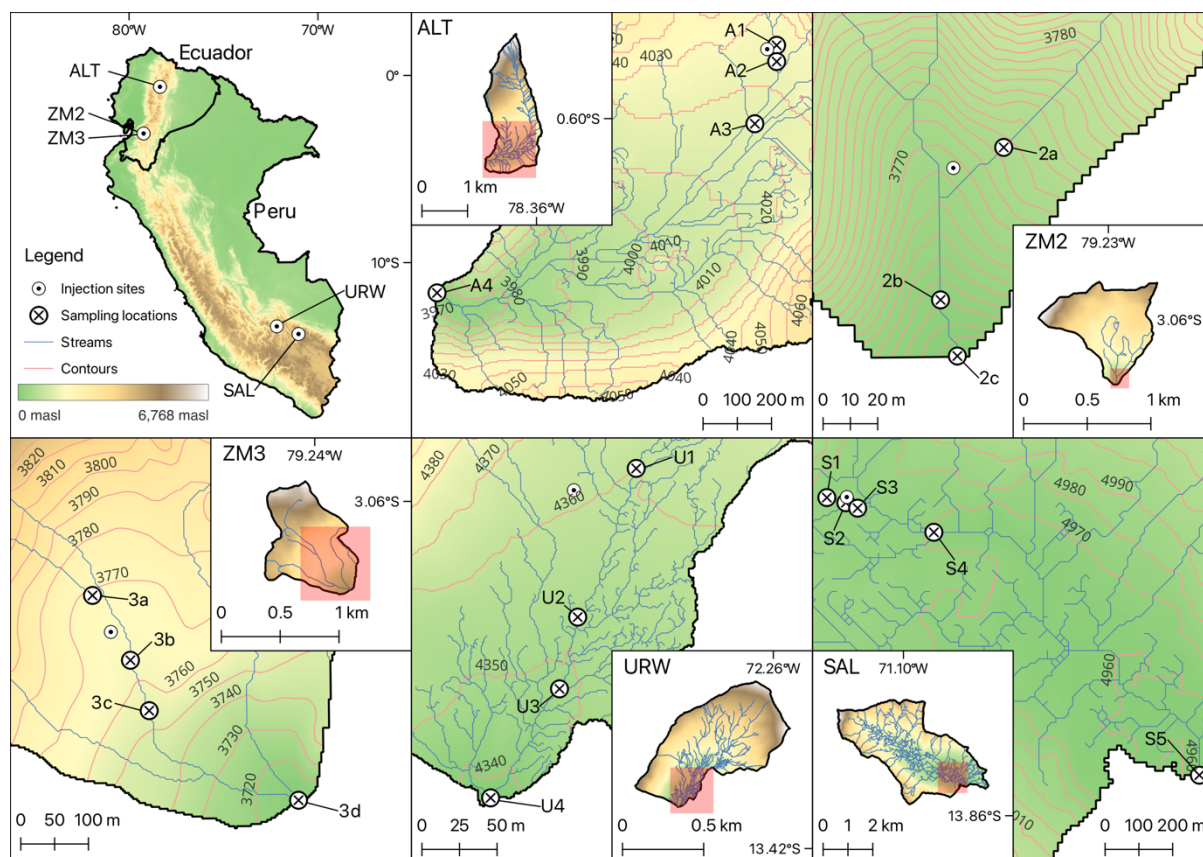
2 Materials and methods

2.1 Study region

We conducted our experiments in five alpine wetland-dominated headwater catchments to isolate wetland-stream connectivity across Ecuador and Peru (Table 1, Figure 1). The sites are located in 2 types of alpine biome found in the Andes, known as Páramo (ALT, ZM2, ZM3) and Humid Puna (URW, SAL). These biomes are both composed of high-Andean grasslands that exist between the forest line (3000-3500 m asl) and the permanent snowline (4700-5300+ m asl) (Fox and Bloom, 1994; Klein et al., 1999; Francou et al., 2004; Buytaert et al., 2006; Cuesta et al., 2009; Céleri et al., 2010; Bromley et al., 2011; Basantes-Serrano et al., 2016). Climate in the Ecuadorian Páramo is driven primarily by continental and tropical Atlantic air masses from the east as well as by the Pacific coastal regime from the west (Vuille et al., 2000; Esquivel-Hernández et al., 2019; Zhiña et al., 2022). Precipitation has a relatively homogeneous distribution with a predominance of long and low-intensity events, occurring throughout the year, with slightly wetter periods from March to May and drier periods from August to October (Padrón et al., 2015). In contrast, sites in the Humid Puna experience a highly pronounced seasonality with 85-99% of annual rainfall occurring between October and April (Wunderlich et al., 2023; Gribbin et al., 2024).

Table 1: Study sites.

Site name	Site Code	Outlet coordinates	Area [km ²]	Elevation Range [m asl]	Annual rainfall [mm year ⁻¹]
Altopita	ALT	00° 36' 28" S 78° 22' 12" W	2.41	3965 – 4227	837 (2018-2025; FONAG, no date)
Zhurucay micro-catchment 2	ZM2	03° 03' 45" S 79° 14' 04" W	0.39	3761 – 3910	1222 ± 22 (2011-2018; Larco et al., 2023)
Zhurucay micro-catchment 3	ZM3	03° 04' 00" S 79° 14' 15" W	0.49	3713 – 3918	1222 ± 22 (2011-2018; Larco et al., 2023)
Upper Ramuschaka Watershed	URW	13° 25' 19" S 72° 16' 10" W	0.38	4337 – 4528	803 ± 3 (2019-2021; Wunderlich et al., 2023)
Sibina Sallma	SAL	13° 50' 57" S 71° 04' 37" W	13.13	4958 – 5520	776 (2017-2021; Ross et al., 2023)



115 **Figure 1: Locations of study sites (Table 1) within Ecuador and Peru (top left). Topographic maps of each study site, showing**
injection and sampling locations (other tiles).

The main soil types at the Ecuadorian sites are Andosols and Histosols (Crespo et al., 2011). Andosols are mainly located on the hillslopes and usually covered by tussock grasses (*Calamagrostis* and *Festuca*) whereas Histosols are found in valley
120 bottom wetlands that sustain cushion plants (*Plantago rigida*, *Xenophyllum humile*, and *Azorella* spp.) (Ramsay and Oxley, 1997; Sklenář and Jørgensen, 1999; Mosquera et al., 2015; Larco et al., 2023). In Zhurucay sites, depth to bedrock, formed of compacted and fractured volcanic and volcanoclastic rock deposits (Coltorti and Ollier, 2000; Hungerbühler et al., 2002; Jerves-Ramirez et al., 2026), is 0.9-2.0 m for Histosols and 0.2-0.7 m for Andosols (Lazo et al., 2023). We do not have
125 specific information on the depth to bedrock at ALT; however, given its location within the recent volcanic formations of the Ecuadorian Andes (Hall and Mothes, 2008), soil depth is believed to be far greater than at Zhurucay sites. Páramo soils have a typical bulk density of $\sim 0.3 \text{ g cm}^{-3}$ and a saturated hydraulic conductivity of $\sim 15 \text{ mm h}^{-1}$ (Buytaert et al., 2005).

Wetlands in the Humid Puna are known locally as bofedales and are similarly inhabited by low growing hydrophytic cushion plants (Wunderlich et al., 2023). Their organic-rich soils have observed depths of 0.6-1.75 m in URW (Wunderlich et al.,



2023) and 0.3-1.25 m in SAL (Ross et al., 2023), which is within a similar range observed by other local studies (0.5-1.5 m; King et al., 2021; Perez and Loisel, 2023; Gribbin et al., 2024). The studied wetlands in this region overlay a low-permeability clay-rich lacustrine deposit (Ross et al., 2023; Wunderlich et al., 2023) which likely promotes their formation (Glas et al., 2018). Wunderlich et al. (2023) reports a mean porosity of ~0.88 and a saturated hydraulic conductivity of ~596 mm h⁻¹ in the peat layer of URW. Oyague et al. (2022) reports a saturated hydraulic conductivity of 1.25-23.75 mm h⁻¹ at high-mountain wetland sites found in central Peru.

2.2 Experimental set up

2.2.1 Hydrometric monitoring

Three fully perforated observation wells were installed in close proximity to each other (< 2 m) at each wetland site at depths of at least 1 m or until the bedrock was reached. One well in each site was fitted with either an ultrasound logger or a pressure transducer to measure water tables, apart from at ALT where only manual measurements were taken. Regular manual measurements were also taken in ZM2, ZM3 and SAL sites to supplement automated data collection. Each catchment was fitted with at least one rain gauge. Access constraints restricted us from downloading rainfall data at SAL, so we used data from the Sibinacocha weather station (< 20 km away; SENAMHI, 2026). Stream levels were recorded at the outlet of each site with either an ultrasound logger or a pressure transducer and rating curves were fitted using salt dilution streamflow measurements. Heavy bank erosion significantly changed the cross-section at SAL, preventing us from developing a reliable rating curve and estimating streamflow.

2.2.2 Tracer dye experiments

Fluorescent tracing experiments and lab analysis were conducted following protocols from the Ozark Underground Laboratory (Aley and Beeman, 2015; Aley, 2019). 907 g of fluorescein was injected at each site, split between the three wells. We used the same mass as Ochoa-Tocachi et al. (2019) as it achieved downstream detection after several months without causing visible pollution. The dye, in powdered form, was dissolved in about 5 litres of water. Wells were bailed and the dye solution was carefully poured in. Sampling locations were identified prior to injection and activated carbon samplers, containing 4.25 g of Barnebey and Sutcliffe Type AC Activated Carbon with a surface area of 1,150 m² g⁻¹, were installed in streams to measure accumulated dye, 1 upstream of dye injection to measure background fluorescence and 2-3 downstream. These were collected and replaced at variable time intervals due to operational reasons (usually every 1-2 weeks; Tables S1-6). Samples were kept in dark and cool conditions until laboratory analysis to limit dye degradation.



2.3 Analysis

2.3.1 Laboratory analysis

Each sampler was washed in jets of DI water, to remove sediment and organic matter, and the enclosed charcoal was soaked in 15 ml of eluting solution for 1 hour to extract the dye. The eluting solution contained 67% isopropyl alcohol, 1% ammonia and 32% water, mixed with sufficient potassium hydroxide pellets to saturate the solution. All glassware was acid washed prior to each use. Eluted solutions from each sample were poured into separate disposable screwcap sample bottles and kept in the freezer. Samples were analysed on a Varian Cary Eclipse benchtop fluorescence spectrophotometer (Agilent Technologies, Inc.) with a synchronous scan of excitation (445-560 nm) and emission (475-550 nm) spectra. An excitation/emission wavelength pair of 500/519 nm was selected as this gave consistently the highest intensity peak value during analysis of calibration standards and are within known ranges of fluorescein excitation and emission spectra (Lakowicz, 2006). Calibration standards 0-40 $\mu\text{g l}^{-1}$ (representing the full range of sample concentrations) to convert intensity to concentration were prepared by mixing the fluorescein powder used in the experiments with the eluting solution and were analysed at the start and end of each day (Howard et al., 2022). The 10 $\mu\text{g l}^{-1}$ standard was analysed every 10 samples to account for drift. Analysis using the fluorescence spectrophotometer was undertaken on two sets of dates: 15-16/04/2025 and 01/10/2025. A linear equation was fitted between calibration standards and fluorescence intensity for each set of dates ($R^2 = 0.99$ and 0.99 , respectfully)

2.3.2 Data analysis

Accumulated dye concentrations were estimated from intensity for each sample using the calibration equation from the date that the sample was analysed. A positive response must have a narrow peak between 515 and 520 nm, typical of fluorescein, rather than low, broad peaks more typical of background fluorescence (Aley and Beeman, 2015). We analysed the emission spectra of all samples, including control samples. We also analysed the spectra of each sample minus the spectra of the associated control sample, assuming that it was representative of background fluorescence. We analysed spectra with and without control spectra subtracted since background fluorescence can vary substantially across river basins, even along the same channel, due to spatial differences in dissolved organic matter compositions and sources along a stream (Lambert et al., 2016; Zhao et al., 2017; Han et al., 2021; Lupon et al., 2023). An analysis of these spectra to determine positive fluorescein responses is provided in the supplementary material (Tables S1-6). The experiments at ZM2, ZM3 and SAL showed evidence of contamination, as positive responses were observed in some of the control samples. We identified possible sources of contamination and attempted to separate them from the genuine responses (Appendix A).

For the purpose of comparing between experiments, we estimate an approximate “travel time” as the number of days between the injection date and the sample date with the peak fluorescein concentration (calculated in ppb/day). A range is given between the previous sampling date and the peak sampling date, as the peak could have occurred at any point during



this time. Where multiple distinct peaks are seen, multiple travel times have been estimated. Stream connectivity is assessed by whether we observe a positive response in the downstream sampling locations during the sampling period. We combined our data and analysis with the literature to identify the connectivity mechanisms between wetlands and streams and discuss their controls. This was used to develop a perceptual model to inform future modelling approaches to assess wetland-stream connectivity mechanisms and governing processes in high-mountain contexts.

3 Results and discussion

3.1 Overview

All sites show distinct and clear responses except ALT, which shows a much lower, possibly negligible response many weeks later than at other sites (Table 2). The small, possibly absent response at ALT may have several explanations. It may indicate that the wetlands were not connected to the stream during the sampling period, that the travel time was longer than the sampling period, or that the dye took a route that bypassed the sampling locations altogether. It is also possible that high levels of organic matter in the soils could have accelerated dye absorption (Bork et al., 2020), preventing it from travelling to the stream. The other sites show a clear seasonality. Positive responses were seen much earlier and consistently during the wet season experiments, while the dry season responses show a delay of at least one-to-two months before positive responses. Dye was found to be visibly present in wells months after the sampling procedure at each site, indicating high local water retention in the studied wetlands. It could also indicate that wetlands are not well-mixed, that preferential flows dominate the hydrological response or that the mean travel time was not captured during the sampling period. A full report for each experiment, including analysis of the fluorescent tracing results against rainfall-runoff data and wetland water levels, describing any contamination concerns and their implications, can be found in Appendix A. Here, we describe how our results provide evidence of the connectivity mechanisms between wetlands and streams (surface runoff, shallow and deep subsurface flow) and discuss their controls.

Table 2: Fluorescent tracer dye results. Sampling locations in bold (in the “Distance: injection to sampler” column) indicate where positive or possibly positive samples were collected (not including samples with high likelihood of contamination). Results in italics indicate only possibly positive samples. Contamination was assessed by whether a positive response was found in the control sample.

Site code	Date of dye injection	Positive response?	First response	Peak response(s)	Travel time(s)	Distance: injection to sampler	Contamination concerns?
ALT	03/06/2024 (dry season)	<i>Maybe</i>	02/10/2024- 16/10/2024	02/10/2024- 16/10/2024	121- 135+ days (if positive)	A1: 20 m A2: 40 m A3: 219 m A4: 1.2 km	No



ZM2	07/06/2024 (dry season)	Yes	16/08/2024- 30/08/2024	16/08/2024- 30/08/2024	70-84 days	2A: 25 m 2B: 50 m 2C: 64 m	Yes but likely unrelated
ZM3	07/06/2024 (dry season)	Yes	31/07/2024- 07/08/2024	07/08/2024- 16/08/2024	61-70 days	3A: 59 m 3B: 43 m 3C: 122 m 3D: 362 m	Yes but likely unrelated
URW	06/01/2025 (wet season)	Yes	06/01/2025- 12/01/2025	06/01/2025- 12/01/2025 19/01/2025- 26/01/2025 10/03/2025- 22/03/2025	0-6 days 13-20 days 63-75 days	U1: 44 m U2: 84 m U3: 133 m U4: 212 m	No
SAL	24/06/2024 (dry season)	Yes	28/07/2024- 04/08/2024	No distinct peak, positive responses continue until end of sampling	34-62+ days	S1: 60 m S2: 4 m S3: 38 m S4: 266 m	Yes
	11/01/2025 (wet season)	Yes	11/01/2025- 25/01/2025	11/01/2025- 25/01/2025 08/02/2025- 22/03/2025	0-14 days 28-70 days	S1: 60 m S2: 4 m S3: 38 m S4: 266 m S5: 1.3 km	Yes

3.2 Connectivity mechanisms

3.2.1 Surface runoff

220 Saturation-excess is the dominant overland flow mechanism in natural high-Andean catchments and studies have shown that infiltration-excess is almost completely absent (Buytaert et al., 2006; Buytaert and Beven, 2011). This suggests that an overland connection to streams is likely only present during sustained wet periods. Wunderlich et al. (2023) notes the likelihood of overland flow at URW during a ‘steady-state’ phase when wetlands are saturated (as shown in the injection well between March and May, Figure 2). Our wet season experiments show an immediate and sharp peak in dye concentration on the first sampling date (Table 2, Figure 2; 6 days after injection at URW, 14 days at SAL). The length of time between sampling makes it difficult to attribute positive responses entirely to surface runoff. However, high water

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230 levels and ponding of dye around the wells on the day of injection (by filling the wells to surface level) could have caused a fill-spill effect. Further evidence of this is seen at URW where a third peak occurs during a sustained period of very high water levels and continued rainfall, also demonstrating a possible fill-spill mechanism. The fact that dye is still visibly present in wells months after sampling could show that fill-spill hydrology is dominant in these systems and that local subsurface dispersion is minimal. Fill-spill events occur when water levels in wetlands rise due to increased rainfall and subsurface inflow during sustained wet periods, causing surface pooling and an overland connection to streams. Threshold-triggered connectivity between normally disconnected water storages and streams have been identified in Andean wetlands (Buytaert and Beven, 2011). This process has also been documented in Prairie wetland complexes in North America (Leibowitz and Vining, 2003; Shaw et al., 2012).

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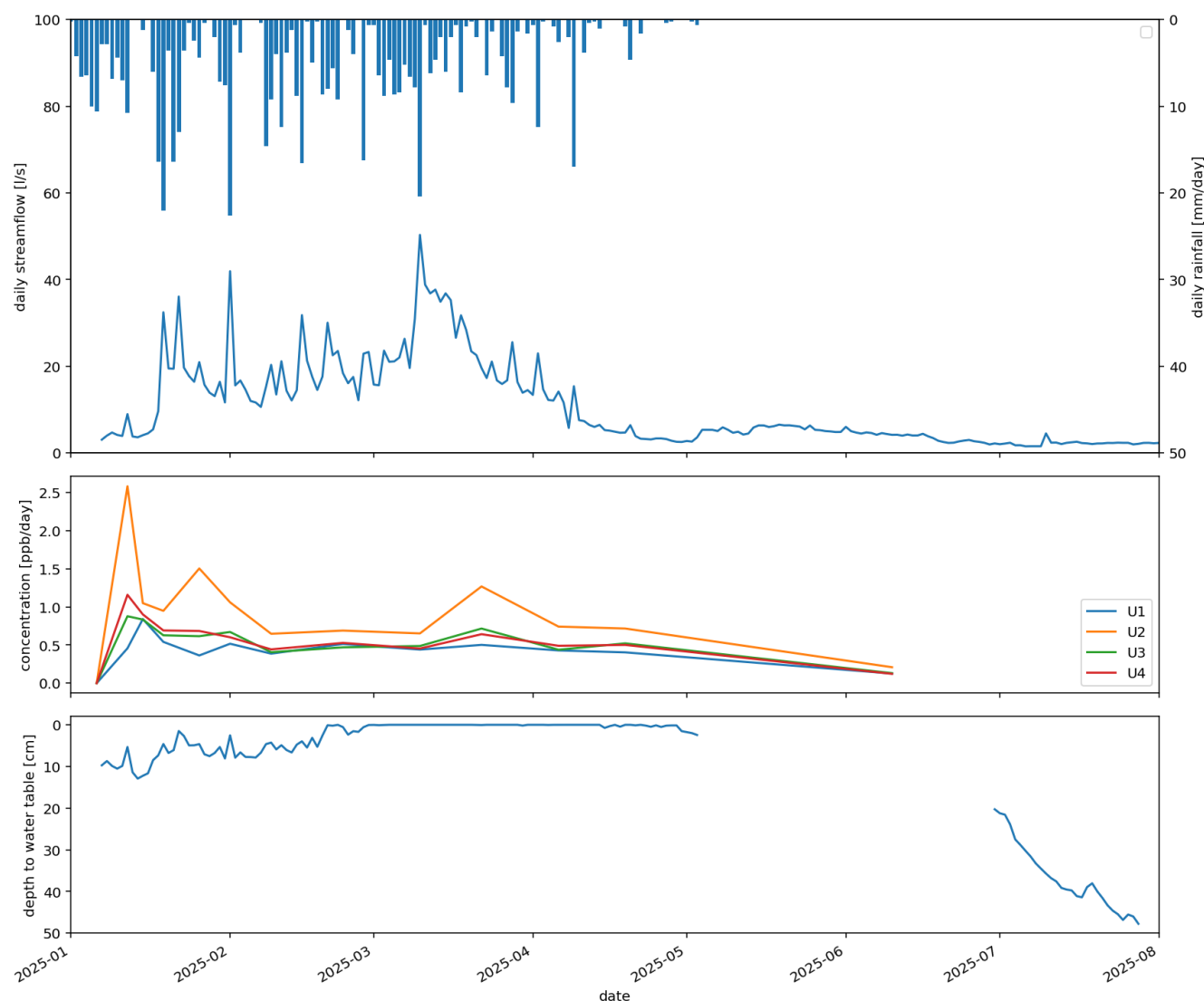


Figure 2: Daily streamflow and rainfall (top), accumulated dye concentration per day between sampling dates at sampling locations (middle), and depth to water table at injection well (bottom) at the Upper Ramuschaka Watershed (URW). The point at which the concentration graphs begin is the date of injection (06/01/2025).

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3.2.2 Shallow subsurface flow

Shallow subsurface flows are dominant across high-Andean wetlands (Correa et al., 2017; Cooper et al., 2019; Wunderlich et al., 2023; Gribbin et al., 2024; Mosquera et al., 2016a) and in Scottish montane peatlands (Soulsby et al., 2011; Tetzlaff et al., 2014; Geris et al., 2015). Our results show that wetlands continue to contribute to streamflow with multiple peaks in dye concentration throughout the wet season (e.g., Figure 2). Sustained, non-sharp responses are more indicative of a continuous

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subsurface contribution. Wetland levels are not as high in the second peak at URW as they are for the third (Figure 2), suggesting that the second peak is less likely caused by a fill-spill overland flow process. The relatively short travel time of this response indicates a shallow subsurface route through the wetlands, rather than a deeper groundwater route, with peaks in concentrations possibly being caused or at least enhanced by increased inflow to wetlands, demonstrating a ‘piston flow’ like process. This process occurs when increased inputs from rainfall and subsurface inflow to wetlands cause water levels to rise and increase hydraulic gradients. For example, wetland level rise between the 2nd and 3rd peak at URW (Figure 2) indicates increased contributions from hillslopes. This could increase subsurface outflow rates pushing pre-event or old water from the wetlands into streams (Correa et al., 2017; Lazo et al., 2019; Mosquera et al., 2016a). It could explain the quicker travel times in the wet season and slower in the dry season, indicating that wetlands may have dynamic residence times that depend on wetland storage and inflow (Tetzlaff et al., 2014). It explains the sustained contributions to flow during the wet season when wetland inflow is consistently high. Several peaks in dye concentration could be caused by variable influxes and wetland levels throughout the experiment. In drier periods, wetlands receive less inflow and probably suffer a higher rate of evapotranspiration and recharge losses, therefore, contributing slower and less to headwater streams. Another possible cause for the multipeak response in wet season experiments could be preferential flows followed later by a slower soil matrix response or variable subsurface flux through different media with different hydraulic conductivities, such as clay and peat.

3.2.3 Deep subsurface flow

Connection to deep groundwater is believed to be minimal in several wetland sites across our study region due to highly impermeable bedrock (Buytaert et al., 2005; Buytaert et al., 2007; Lazo et al., 2019; Rodríguez-Morales et al., 2019; Mosquera et al., 2016a). Jerves-Ramirez et al. (2026), however, demonstrates high connectivity between wetlands and deeper groundwater due to well-developed fracture networks in the region of ZM2 and ZM3. Additionally, at a site close to ALT, evidence shows that vertical fluxes are dominant in wetlands with thick volcanic ash soils and permeable bedrock (Lahuatte et al., 2022). Multiple peaks in our wet season experiments could be explained by divergent routing, i.e., different flow paths from the point of injection via quicker and slower subsurface routes. The travel time of the final peak in URW is similar to that seen in the dry season experiments (Table 2, Figure 2). This could be a result of the dye following a deeper subsurface route in both cases. Since wetland levels drop substantially, shallow subsurface routes may not be available or as active during the dry season, meaning that the delayed breakthrough curves could be caused by deeper subsurface connections between wetlands and streams. This could be a deep soil layer (Buytaert et al., 2004; Pesántez et al., 2023a) or a deeper route through the bedrock (Lahuatte et al., 2022; Jerves-Ramirez et al., 2026). It should be noted that recharge from wetlands to deep groundwater is more likely during wet periods due to increased vertical hydraulic gradients (Jerves-Ramirez et al., 2026) and that if any dye did make its way into a deeper groundwater system, it may have followed a route that bypassed the sampling locations altogether (e.g., Gleeson and Manning, 2008; Frisbee et al., 2011; Hayashi, 2020) or that had a larger residence time than covered by our sampling periods.



3.3 Connectivity controls

280 3.3.1 Topography

Many mountain wetlands are characterised by complex micro-topographies where saturated areas are often disconnected from each other and the stream network (e.g., Buytaert and Beven, 2011). Lane et al. (2004; 2009) show that there must be sufficient saturation along an entire flow path towards a stream to maintain an overland connection. The propensity to connect and the duration of connection is determined primarily by the topographic wetness index along the entirety of this path combined with the level of actual catchment wetness (Lane et al., 2009). Lane et al. (2009) also notes that this should apply equally for shallow subsurface flows. This is evident, since a fill-spill event in a wetland that does not form or maintain an overland connection to streams likely still enhances shallow subsurface recharge and flow.

3.3.2 Subsurface geology and soils

Underlying geology and soils also have a significant control on wetland connectivity to streams. Wetlands that have deeper soils or permeable bedrock may incur larger losses to recharge, contributing a more significant proportion to groundwater flows (Birkel et al., 2011; Soulsby et al., 2011; Lahuate et al., 2022). Deep groundwater recharge may be a dominant process at ALT where we see little to no response many weeks later than at other sites. Fractured bedrock may encourage a strong connection between wetlands and deep groundwater at ZM2 and ZM3, however, shallow subsurface flows still dominate (Jerves-Ramirez et al., 2026). In wetlands formed over low permeability bedrock with thinner layers of soil, found at our remaining sites, shallow subsurface flows are dominant and recharge to deeper groundwater can be negligible (Buytaert et al., 2005; Buytaert et al., 2007; Soulsby et al., 2011; Lazo et al., 2019; Rodríguez-Morales et al., 2019; Mosquera et al., 2016a). Davies et al. (2026) demonstrates, at a site close to SAL, that geology creates the poor drainage conditions required for the development of many wetlands by providing topographic barriers of bedrock or moraines. The permeability of these barriers control the dominant connectivity mechanism to the stream. A wetland may only be able to connect via fill-spill hydrology if impermeable, otherwise, there could be a stronger subsurface connection.

Soil types and layers provide an additional control on connectivity, demonstrated in Buytaert et al. (2004) and Pesántez et al. (2023a), where two subsurface response times, seen also in our wet season experiments, correspond to distinct soil layers (Histic Andosols and Histosols). Dye being visibly present in wells months after sampling may demonstrate that these lower layers could be much less hydrologically active than the upper horizons where the majority of flow may occur. Macropore or preferential flow versus matrix flow, controlled by soil structure, could provide an alternative explanation for the persistence of dye in the wells, and for the multipeak response in our wet season experiments.



3.3.3 Hydrometeorological conditions and connectivity to groundwater

Wetland levels control the routes that water can take. When levels are low, wetlands become increasingly disconnected and
310 only deeper subsurface routes or vertical fluxes, via evapotranspiration or recharge, may be available. When levels are
raised; quicker, shallow subsurface and overland routes become available, given that there is a clear, unobstructed and
sufficiently saturated path to a stream. Low water levels seen during our dry season experiments, especially at ALT, likely
inhibit shallow subsurface and overland routes to the stream. Higher levels, seen in our wet season experiments, activate
these routes resulting in faster travel times between wetlands and streams. Wetland levels also determine the hydraulic
315 gradient, alongside surface and bedrock topography, which controls the rate at which water moves through wetlands.

Wetlands can be recharged by rainfall, hillslope subsurface flow or groundwater (Cooper et al., 2019; Jerves-Ramirez et al.,
2016) and water levels can only remain high if inflows are high enough to offset outflows and losses. Close to ZM2 and
ZM3, Jerves-Ramirez et al. (2026) demonstrates that wetlands' connectivity to streams during drier periods depends on
320 whether they are sustained by groundwater or not. Wetlands that are not sustained by groundwater will eventually disconnect
from the stream network as water levels start to drop. Groundwater-fed wetlands, on the other hand, may stay sufficiently
saturated and continue to contribute to streamflow. The ability for a wetland to maintain high water levels during extended
dry periods, therefore, relies on the upslope groundwater table, its connectivity to wetlands and its conductivity to be able
recharge wetlands effectively.

325 Though admittedly difficult to characterise whether a wetland is sustained by groundwater, springs that feed wetlands can be
observed at various sites. For example, Gribbin et al. (2024) and Davies et al. (2026) identify several springs that sustain
groundwater supplies to bofedal wetlands in the Cordillera Vilcanota (where SAL is located), maintaining a continued
connection between wetlands and streams during the marked dry season characteristic of the region. Similar springs have
330 been identified in URW (Moore et al., 2026) and ZM3. Davies et al. (2026) also notes a likely connection to the underlying
glaciofluvial aquifer in riverine wetlands found in the Cordillera Vilcanota, which may act as a water source or sink for
wetlands. Classification of landforms, such as talus cones, moraines and alluvial fans, upstream of wetlands can help to
identify whether they are likely to be sustained by hillslope and groundwater flows (Davies et al., 2026). Measuring
electrical conductivity in wetlands can also give us an indication of whether they are predominantly groundwater fed (e.g.,
335 Lazo et al., 2024).

3.4 Improving wetland-stream connectivity in hydrological models

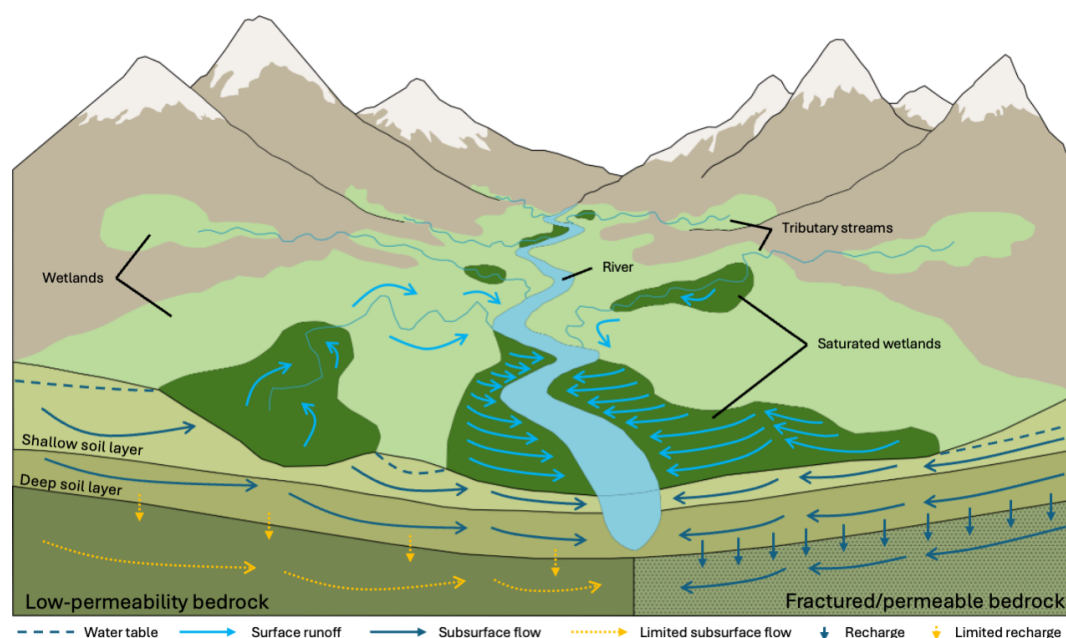
The structure and governing equations in hydrological models such as Ross et al. (2023), that incorporate and conceptualise
wetland functioning, could be improved by simulating the connectivity mechanisms and their controls highlighted in our
perceptual model (Figure 3). Multiple model structures that test our different hypotheses, following a similar methodology to



340 Buytaert and Beven (2011) and Pesántez et al. (2023a), could be applied across several representative wetland-dominated catchment sites to assess which structures and equations best characterise the system under different conditions. This should be combined with in-depth topographic (using high-resolution DEMs), geological and hydrometeorological analyses, to provide a deeper, process-based understanding of the connectivity mechanisms between wetlands and streams and their controlling factors, allowing us to extrapolate our findings to less monitored regions. Our experiments could be expanded to

345 further investigate the temporal and spatial controls on wetland connectivity by using several dyes in conjunction (such as fluorescein, eosin, sulforhodamine b and rhodamine wt; Aley, 2019). Dyes could be injected at the same time into multiple wetlands that feed the same stream to assess divergent behaviours, or they could be injected into the same wetland at different times throughout the year to further evaluate temporal and climatic controls. In wetlands with deep soils, dyes could be injected at multiple depths to disentangle the relative contributions of shallow and deep subsurface flow paths. In

350 addition, these experiments could be combined with natural tracers, including isotope analysis or electrical conductivity, to provide complementary insights into mixing processes and water age and help to improve understanding of connectivity mechanisms such as piston and preferential flow processes.



355 **Figure 3: Perceptual model of high-mountain wetland-stream connectivity mechanisms and governing processes. The diagram highlights that the water table controls which routes are available. Surface runoff can only occur over saturated wetlands and its connectivity to streams is determined by whether there is a saturated route to a stream. This is controlled by topography and catchment wetness. Disconnected wetlands may contribute to streamflow via tributary streams or creeks and subsurface routes only after reaching a certain level of saturation. There is a marked reduction in recharge losses and deep groundwater flow in wetlands overlaying low-permeability bedrock, compared to those underlain by fractured or highly permeable bedrock. Finally, deep groundwater may or may not contribute to streams at the headwater scale.**

360



4 Conclusions

We built a perceptual model of high-mountain wetlands' connectivity to streams by employing fluorescent tracing techniques combined with rainfall-runoff and wetland water level monitoring across five high-altitude study sites from northern Ecuador to southern Peru. We observed travel times between wetlands and streams from less than 1 week to upwards of 3½ months, with one site showing little to no response during the sampling period. Despite the highly variable travel times, continued fluorescein responses seen months after dye injection at most sites demonstrate the significance of wetlands to year-round water supply and regulation. Our analysis provides evidence of three connectivity mechanisms between wetlands and streams (surface runoff, shallow subsurface flow and deep subsurface flow), and identifies topographic, geological and hydrometeorological controls on these mechanisms. Future studies should leverage the injection of multiple dyes within the same site to quantify climatic and topographic controls on wetland connectivity. In addition, model structures that reflect our findings should be implemented across several sites to further evaluate our hypotheses and assess the feasibility of regionalisation. This would allow us to extrapolate and scale our insights to include under monitored regions and improve their relevance at the international level.



375 Appendix A

Altopita (ALT)

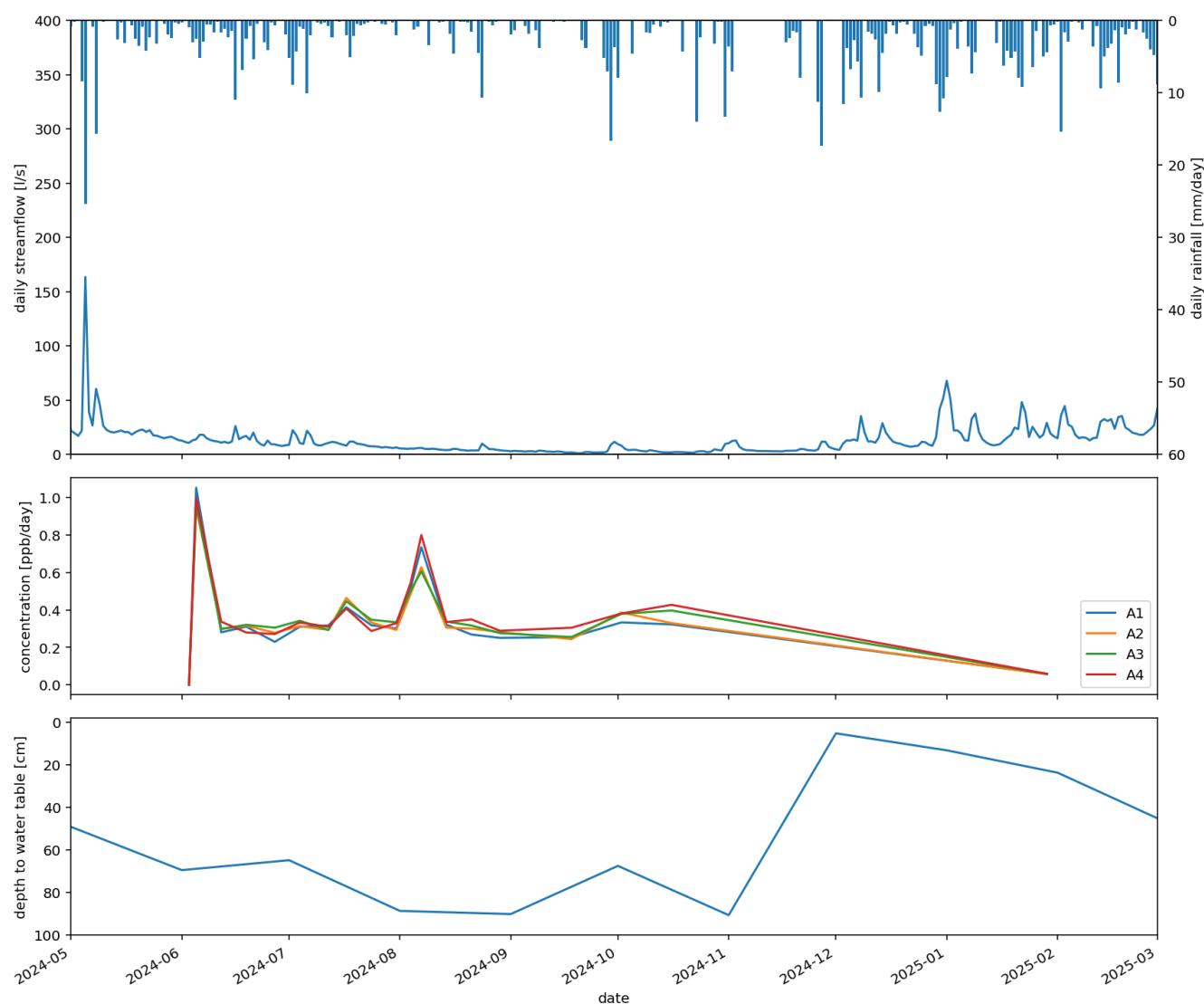


Figure A1: Altopita (ALT) data. Daily streamflow and rainfall (top), accumulated dye concentration per day between sampling dates at sampling locations (middle), and depth to water table at injection well (bottom). The point at which the concentration graphs begin is the date of injection (03/06/2024).

380

When scrutinising subject or emission spectra at ALT, small, possible responses are seen in all samples downstream of dye injection collected on 16/10/2024. These peaks are not very significant and are only seen in both subject *and* relative emission spectra at A3. When comparing with control spectra and considering margins of error, these peaks may just be



385 artefacts. This experiment was undertaken during a particularly dry period, and we observe very low water levels in the wetland wells compared to other years, likely causing the wetlands to be far less active and have significantly slower subsurface flowrates with a high possibility that the wetlands were disconnected from the streams altogether within our study site (during the sampling period). This region is known for its deep volcanic soils (Lahuatte et al., 2022), and vertical fluxes may be dominant, meaning that flow from the injection point may have bypassed all sampling locations, resurfacing further downstream. Alternatively, the high organic soil content at this site may have increased absorption rates of the tracer to the point where the remaining dye was undetectable in the stream. Though, if positive, the dye travel time is considerably higher than at all other sites and a lower concentration would, therefore, be expected due to higher amounts of spreading, dilution and absorption in the subsurface. Additionally, we see potential positive responses in the samples collected at A2 and A3 on the following collection date 3½ months later. It is difficult to confirm these responses due to high levels of background fluorescence, however, the small response at 16/10/2024 could be the beginning of a breakthrough curve that occurred during the period between these dates.



Zhurucay Micro-catchment 2 (ZM2)

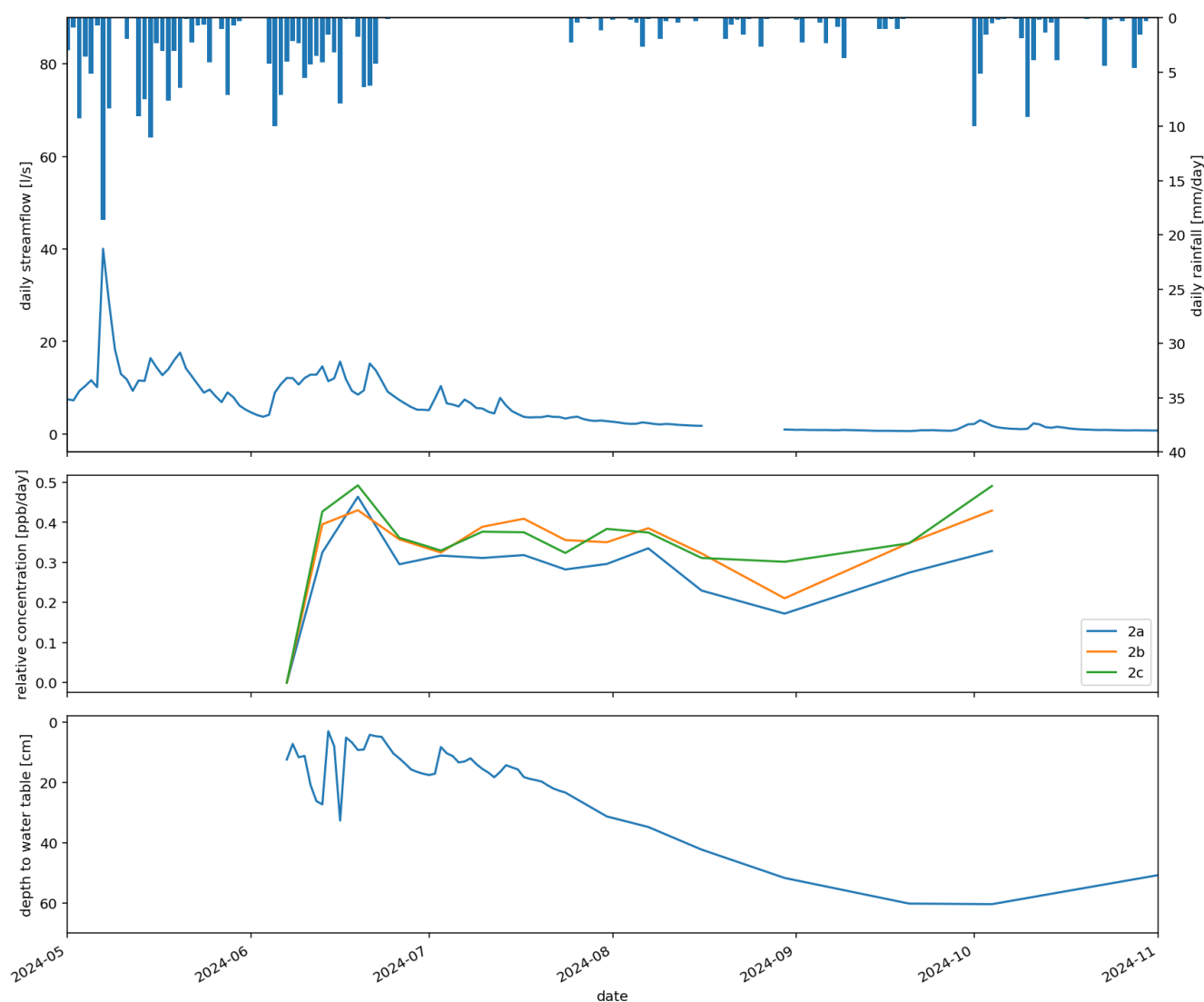


Figure A2: Zhurucay micro-catchment 2 (ZM2) data. Daily streamflow and rainfall (top), accumulated dye concentration per day between sampling dates at sampling locations (middle), and depth to water table at injection well (bottom). The point at which the concentration graphs begin is the date of injection (07/06/2024).

A clear, distinct peak is seen in both the subject and relative emission spectra of the samples collected at 2C on 30/08/2024. We do not see the same response at 2B on that date; however, we do see potential positive responses at 2B and 2C in the following weeks. Samplers at 2B were attached to a submerged rock in a small pool so it's possible that we don't see the same peak due to insufficient mixing. There was an early positive response at 2A in the sample collected on 19/06/2024.



This is believed to have been caused by someone on the sampling team checking the wells before collecting and replacing the sample at 2A. This was reported at the time, and the procedure was corrected for the remaining sampling dates. We do not see positive responses in downstream samples that week or in any of the samples in the following weeks, so we do not
410 believe this contamination to be related to the positive response seen at the end of August.



Zhurucay Micro-catchment 3 (ZM3)

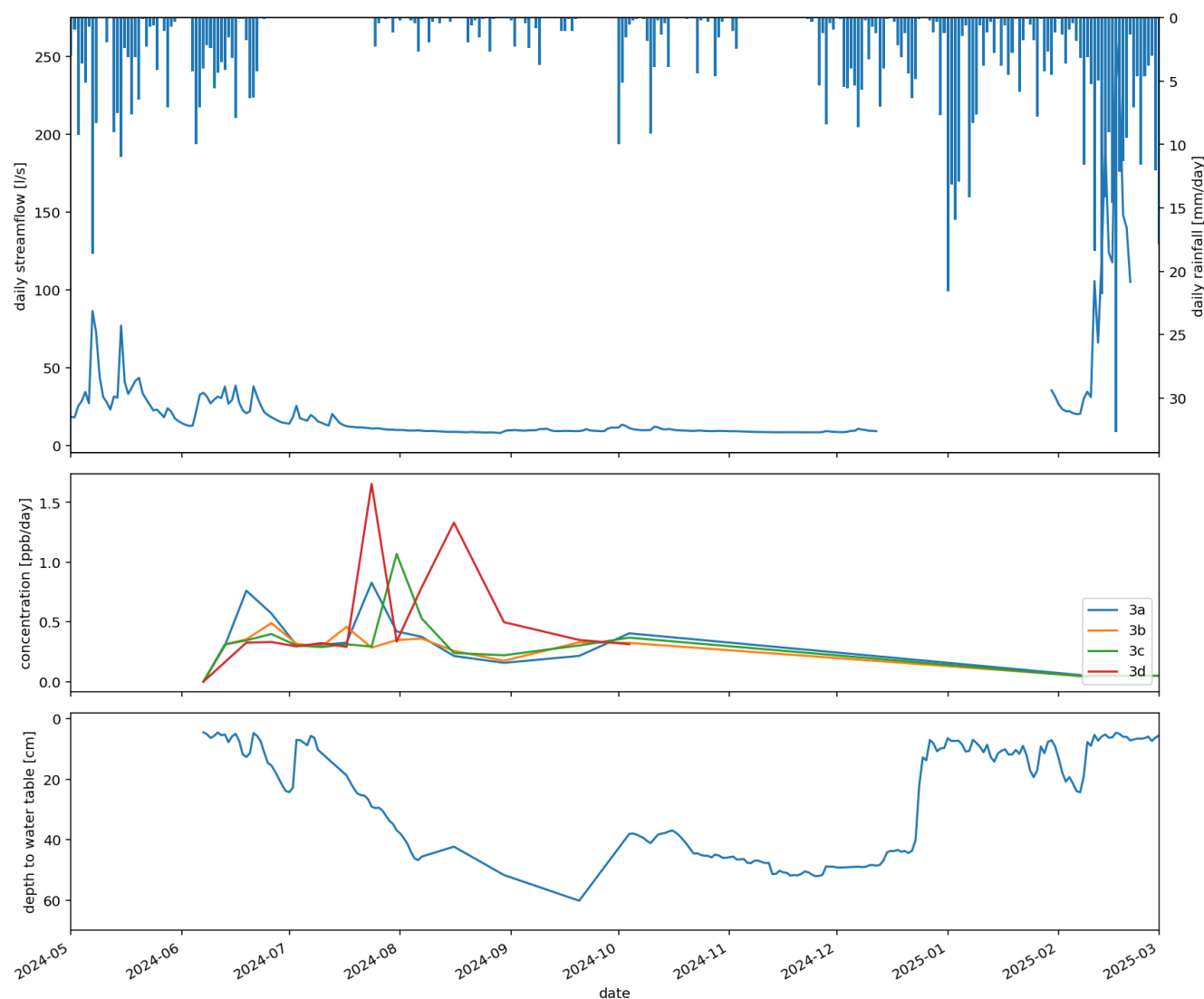


Figure A3: Zhurucay micro-catchment 3 (ZM3) data. Daily streamflow and rainfall (top), accumulated dye concentration per day between sampling dates at sampling locations (middle), and depth to water table at injection well (bottom). The point at which the concentration graphs begin is the date of injection (07/06/2024).

An error in the sampling procedure undertaken by the team at ZM3 became apparent and was rectified between 31/07/2024 and 16/08/2024 (we have not been able to confirm an exact date). They were measuring the dip in the wells before collecting and replacing samples at 3A, 3B and 3C (sampling at 3D was undertaken by a different team). This led to several positive responses in all locations including the control point, therefore, any results before the end of July should be disregarded.



After this date, we see a distinct breakthrough curve in 3D from 31/07/2024 to 04/10/2024 with a peak occurring between sampling dates 07/08/2024 and 16/08/2024. There are small positive responses seen in the samples collected at 3A and 3C on 07/08/2024 which is likely because they were replaced on 31/07/2024 before the procedure was corrected. The values
425 here are much lower than at 3D on the same date, indicating that higher concentrations of fluorescein may have reached 3D via another pathway. Since flowrates at 3D are higher, we would expect lower concentrations here if contaminated by the same source, however, more dye could have made its way into the stream when replacing the sampler at 3C, bypassing this sampler but still travelling to 3D. If the procedure had been corrected by 07/08/2024, all stream contamination should have washed through before this date and not have had any further impact on samples after this date. If the procedure was
430 corrected after this date, then the positive response on 16/08/2024 may have been caused or partly caused by contamination. However, the positive responses after that should not have been affected by contamination. Small, potential responses at 3B and small responses at 3C are dwarfed by the concentrations at 3D. This indicates that most of the flow, from the dye injection point through the wetlands, during this period likely bypassed 3B and 3C. Wetland water levels, rainfall and streamflow remain low, suggesting that the breakthrough curve was fluorescein travelling via subsurface wetland flow, not
435 caused by fill-spill or surface runoff processes.



Upper Ramuschaka Watershed (URW)

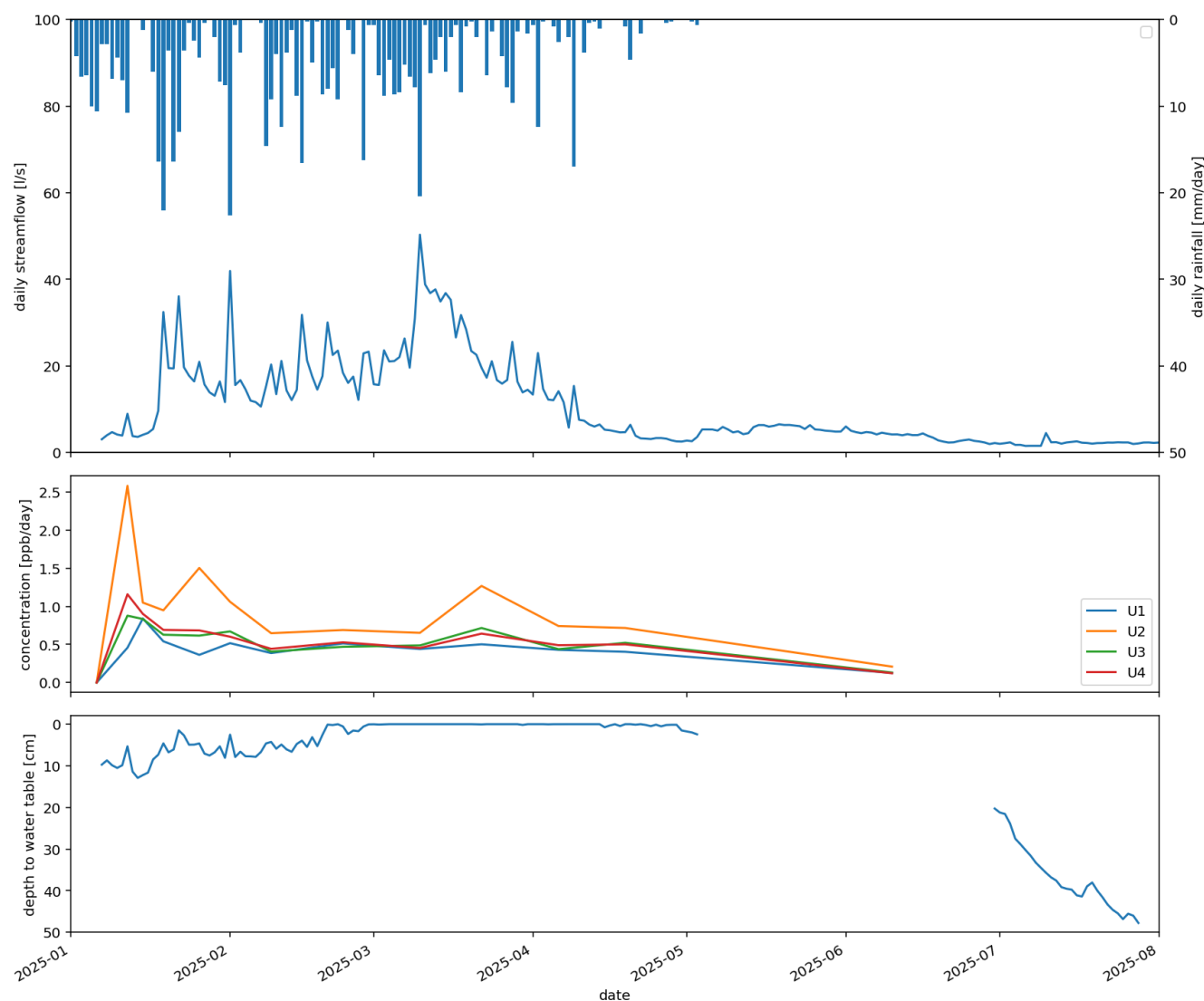


Figure A4: Upper Ramuschaka Watershed (URW) data. Daily streamflow and rainfall (top), accumulated dye concentration per day between sampling dates at sampling locations (middle), and depth to water table at injection well (bottom). The point at which the concentration graphs begin is the date of injection (06/01/2025).

We conducted the experiment at the URW during the wet season. There are three distinct peaks in fluorescein concentration at all sampling locations downstream of the dye injection point. The first is immediate and happens before the first set of samples is taken, 6 days later. The peak is sharp and reduces to lower concentrations in the following weeks. We believe it to be caused by the pooling of dye around the wells during injection, which could have travelled to the stream via overland



flow, explaining the sharp and immediate response. It is also possible that the dye was able to travel to the stream via a subsurface route in under 6 days, indicating a significantly quicker subsurface hydrological connectivity between wetlands and streams. Even the travel time of the second peak demonstrates a much quicker connectivity compared to the other experiments. We believe that the improved connectivity and reduced travel times are caused by seasonality, where higher rainfall and wetland levels increase flowrates from wetlands to streams.

Sibina Sallma (SAL) 2024 dry season experiment

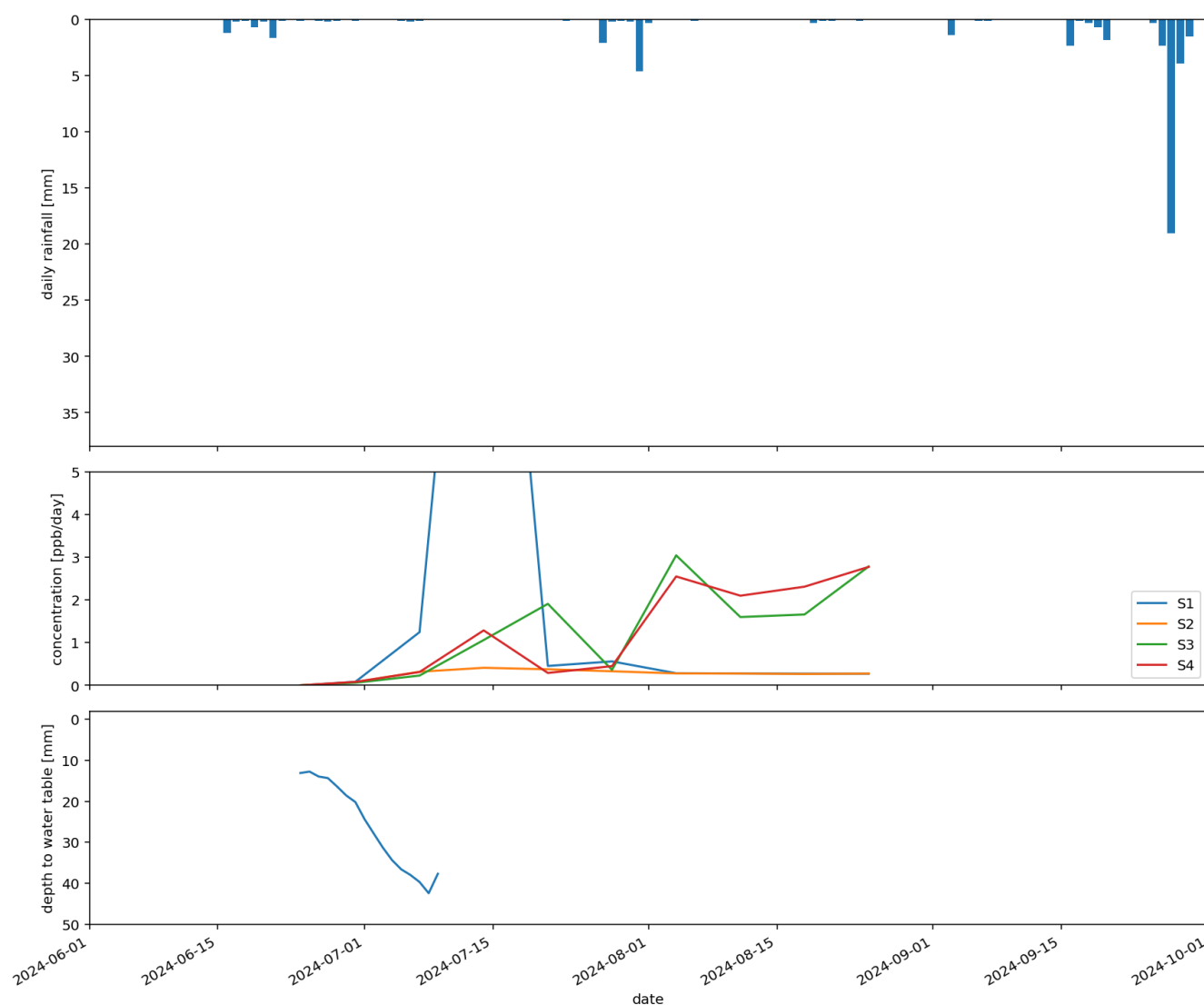




Figure A5: Sibina Sallma (SAL) 2024 data. Daily rainfall (top), accumulated dye concentration per day between sampling dates at sampling locations (middle), and depth to water table at injection well (bottom). The point at which the concentration graphs begin is the date of injection (24/06/2024).

High levels of contamination can be seen in S1 during the first half of the experiment. We believe that this is likely caused by the sampling team measuring the dip in the well before collecting the sample at S1. This could then be responsible for the positive values seen at S3 and S4. S2 hardly responds at all despite it being immediately downstream of the dye injection point. The wetlands here are formed of small pools with connecting small, very slow flowing channels. S2 is located in one of these pools. It's possible, then, that any contamination at S1 may have bypassed S2 via another route. It's also possible that low flow rates in the pool and lack of mixing, combined with high exposure to sunlight (known to degrade fluorescent tracers) may have diminished fluorescent tracer concentrations in the carbon sampler. The contamination at S1 seems to stop from 28/07/2024 and we get a sustained positive response at S3 and S4 from 04/08/2024 onwards. The lack of response at S2 during the entire sampling period, and the route taken by the sampling team, makes it unlikely that positive values at S3 and S4 are related to direct contamination from the wells, but either, a direct route from the wells somehow avoiding a response at S2, or all related to the contamination at S1. In the former case, the breakthrough curves at S3 and S4 could be explained by an immediate response to contamination followed by a delayed response from the original injection. In the latter, more likely case, both quick and slow responses are related to initial and potentially continued contamination. Due to the extreme remoteness of this particular study site, we have not been able to make contact with the sampling team since the laboratory analysis was completed and have not been able to enquire about their specific sampling procedure.



Sibina Sallma (SAL) 2025 wet season experiment

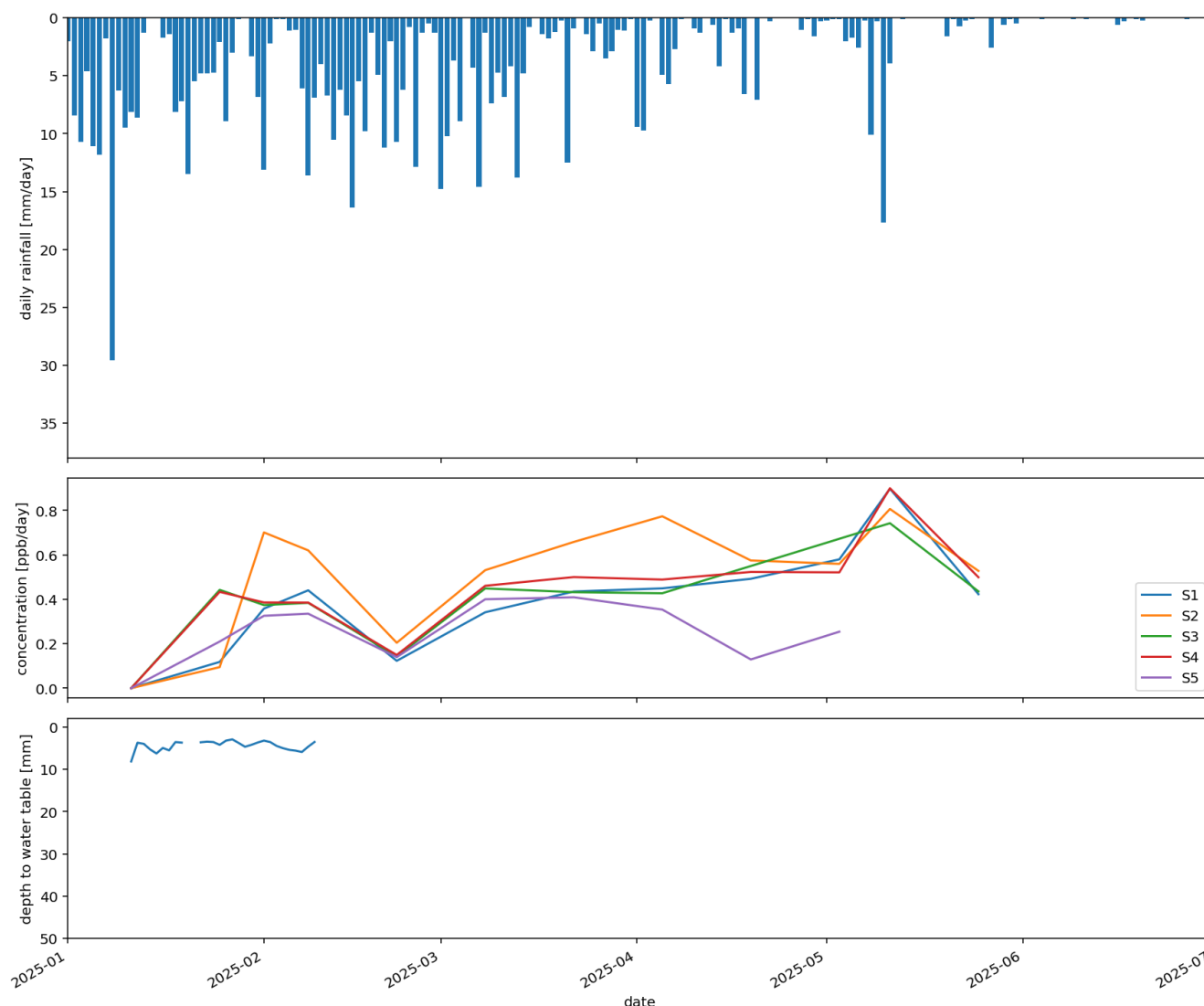


Figure A6: Sibina Sallma (SAL) 2025 data. Daily rainfall (top), accumulated dye concentration per day between sampling dates at sampling locations (middle), and depth to water table at injection well (bottom). The point at which the concentration graphs begin is the date of injection (11/01/2025).

There is an immediate response at all locations downstream of dye injection, particularly in S3 and S4. S2 is much lower and potentially insignificant. It seems unlikely that dye from the wells could have bypassed S2, especially since samples collected here begin to respond significantly from the following date until 05/04/2025. A source of contamination might have occurred downstream of S2 during the date of injection or, since there was still dye in the well from the last experiment,



it may have still be present in the system at concentrations significant enough to impact samples in this experiment. However, if this were the case, we wouldn't expect concentrations at S3 and S4 to reduce as significantly and not show a response on the following dates. Therefore, we believe that the dye had not mixed sufficiently enough in the pool where S2 is located before the first sample was taken but, after that, increased to sufficient levels until 05/04/2025. After this, they begin to decrease and we no longer see sustained responses at this location. We get positive responses at S4 between 08/02/2025 and 22/03/2025 which, after this date, become potential responses. S3 responds similarly but with less distinct peaks in the emission spectra. We obtain one positive response at S1 for the sample collected on 22/02/2025 that could be responsible, in part, for the positive responses downstream. We do not know the source of contamination on this date. No definitive positive responses are seen in samples collected at S5, however, that is likely due to its distance downstream and its significantly increased flowrates compared to other sampling locations. As with URW, multiple peaks are observed in this experiment. In this case, a sharp, immediate response before the first sampling date, and a slower, more sustained response a few weeks later.

Code and data availability

The original runoff, precipitation, wetland water level, and fluorescein tracer concentration data generated during this study and visualised in Appendix A are archived on Zenodo. Reviewers can access these files anonymously during the peer-review process via the temporary token link: [https://zenodo.org/records/21398742?preview=1&token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6IjgyYjk3MDNiLTAzMDEtNDJjNS1iNTUxLWRmMzZwMzAyZTAxOSIsImRhdGEiOnt9LCJyYW5kb20iOiI2NDI5MjBjNzQ1OTc5MjNlOGFmMzMwOGE2OTc2YTU5YSJ9.Lp-Ny4hxZI0JJ7sk8CXbGkOOJ9PKsHKWh9U2LzTLABEAg_T9jw-f5LoYLwxK68n9xAZIAzGzdUiMd0cJQpeQ5Q]. Upon final acceptance of the manuscript, this repository will be made openly public under the permanent DOI: [10.5281/zenodo.21398742]. Meteorological and rainfall data were obtained from the National Meteorological and Hydrological Service of Peru (SENAMHI) and can be requested directly through their official public data request portal at <https://www.senamhi.gob.pe/>.

Supplement link

The link to the supplement will be included by Copernicus, if applicable.

Author contributions

Anthony C. Ross: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing (original draft preparation), Writing (review and editing)



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Competing interests

We declare no competing interests.

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Acknowledgements

The authors would like to give thanks to the community members and field teams at each of the study sites for their continued collaboration, cooperation and facilitation of our research activities. We give special thanks to FONAG and their rangers, UCUENCA and their field technicians and Master's students, and the community members of Zurite and Sibina Sallma in Southern Peru, for their assistance in the implementation of our experiments and subsequent sampling and storage. We are grateful to Adrian Ccahuana Condori, Erick Franklin Gil Rodriguez and Miguel Vargas for driving us to Sibina Sallma and Phinaya and assisting with field activities. ACR expresses sincere gratitude for the continued support and guidance from laboratory technicians, Celia Lima and Kaisheri Guthrie-Fenty, and manager, Geoff Fowler, at the Roger Perry Environmental Engineering Laboratory, Imperial College London. Finally, we give special thanks to the Phinaya and Zurite communities for their generous hospitality and facilitation of our research.

Financial support

This research was supported by the Skempton Scholarship, which provided doctoral funding for ACR, and the Professor Milija Pavlovic Travel Award, which provided financial support for fieldwork logistics and project travel.

Review statement

The review statement will be added by Copernicus Publications listing the handling editor as well as all contributing referees according to their status anonymous or identified.

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