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More Is Not Always Better: Selective Trait Filtering Governs Assembly Under Emerging Flow Intermittency

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ABSTRACT

Flow intermittency is expanding across river networks, transforming perennial streams into newly drying habitats and exposing macroinvertebrate communities to novel selective pressures. Understanding the mechanisms governing community reorganisation under these transitional conditions is essential for predicting ecological responses to climate-driven drying. Using long-term hydrological modelling combined with trait-based analyses along a continuous intermittency gradient, we tested four mechanistic hypotheses addressing taxonomic filtering, trait–state-specific responses, the role of cumulative trait–state advantages and dimension-specific functional reorganisation between resistance and resilience dimensions. Richness declined while Simpson diversity increased with drying, indicating strong but selective environmental filtering (H1). Only specific drying-related trait states increased in representation, revealing differential responses across resistance- and resilience-related states (H2). The number of drying-related trait states did not consistently enhance taxon performance; instead, intermediate and functionally coherent combinations were favoured (H3). Functional richness and redundancy exhibited asymmetric trajectories between the two survival dimensions, highlighting differences in how resistance- and resilience-related strategies reorganise under increasing intermittency (H4). These findings demonstrate that emerging flow intermittency restructures communities through selective trait–state filtering and the dominance of optimal, rather than cumulative, survival strategies. The asymmetric functional trajectories between resistance and resilience dimensions reveal early-stage functional vulnerability in newly drying systems, providing a mechanistic foundation for intermittency-aware bioassessment tools under climate-driven drying.

1 | Introduction

Flow intermittency is rapidly increasing worldwide as climatic variability intensifies and water abstraction accelerates, transforming previously perennial streams into newly drying habitats and leading to the expansion of Drying River Networks (DRNs) (Datry et al. 2021). These hydrological regime shifts expose resident macroinvertebrate communities to ecological constraints that differ fundamentally from those generated by classical anthropogenic stressors. As intermittency alters the temporal structure of habitat availability rather than simply degrading habitat quality, ecological responses cannot be predicted from traditional pressure–response frameworks (Datry et al. 2014).

Flow intermittency acts as a strong environmental filter across DRNs, restructuring aquatic assemblages through changes in hydroperiod, habitat persistence, and connectivity (Bonada et al. 2020; Larned et al. 2010; Szeles et al. 2025). Taxonomic

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richness typically declines and abundance distributions shift as drying intensifies, forming consistent taxonomic signatures of intermittency across diverse climatic regions (Crabot et al. 2021; Datry et al. 2014; Miliša et al. 2022). Beyond species loss, drying also reshapes dominance and, in some systems, evenness (Chanut et al. 2023; Grolimund et al. 2025; Leigh, Boulton, et al. 2016). As environmental filtering in newly drying systems is expected to remove sensitive and often low-abundance taxa first, the resulting loss of rare taxa may reduce dominance asymmetry and lead to a more even distribution of abundances despite declining richness. However, these responses remain largely descriptive. To move beyond description and understand why communities reorganise as they do, mechanistic insight is needed into the functional attributes that mediate persistence and recovery under drying.

A promising path toward such mechanistic understanding is to move beyond trait aggregates and focus instead on trait states (also known as trait modalities or categories)—the discrete functional expressions of traits such as air-independent respiration, diapause, or rapid life-cycle completion. Trait states represent the actual functional units through which environmental filtering operates, and changes in their representation often provide earlier and clearer mechanistic signals than do higher-level functional summaries (Boda et al. 2024). This trait–state perspective is particularly relevant in newly intermittent systems, where selective pressures are novel and emerging, and community responses may differ from those observed in long-established non-perennial streams (Stubbington et al. 2017).

As streams transition from perennial to non-perennial flow, community organisation is governed by two complementary survival dimensions. Resistance enables taxa to persist locally through drying (e.g., dormancy, protective egg structures, small body size), whereas resilience reflects the capacity to recover after rewetting through dispersal or rapid development (Nimmo et al. 2015). Because resistance operates through local persistence mechanisms, whereas resilience depends on recolonisation processes constrained by spatial context and the availability of nearby refugia (Chester and Robson 2011; Datry et al. 2014), these dimensions are expected to show differential sensitivities to increasing drying. Resistance attributes may respond strongly and early as intermittency emerges (Boersma et al. 2014; Verdonschot et al. 2015), while resilience attributes may decline with increasing spatial isolation (Chester and Robson 2011).

A further expectation is that taxa possessing multiple drying-related trait states may gain potential cumulative advantages—the so-called stacking or insurance effect (cf. insurance hypothesis: Yachi and Loreau 1999) – allowing them to cope with heterogeneous drying conditions. Because these trait states represent alternative pathways of persistence or recovery (e.g., surviving dry phases locally or recolonising rapidly after rewetting), taxa possessing multiple drying-related states may maintain higher occurrence or abundance across variable drying regimes. However, such advantages may be constrained by ecological costs or trade-offs among trait states, meaning that possessing more drying-related states does not necessarily translate into higher performance. Instead, the functional coherence of trait–state combinations may be more important than the sheer number of drying-related states.

Environmental filtering may also reshape functional diversity (Robinson et al. 2022). Functional space can contract if only a narrow subset of strategies persists or become reconfigured if alternative combinations remain viable (Bozóki et al. 2024). Because resistance and resilience follow distinct ecological pathways, functional richness, redundancy, and Rao's quadratic entropy may exhibit asymmetric responses across these dimensions. Such asymmetries may serve as early indicators of functional vulnerability in newly drying systems.

Despite increasing interest in DRNs, no study has jointly assessed (i) taxonomic filtering, (ii) trait–state-specific responses, (iii) the role of cumulative trait–state advantages and (iv) dimension-specific functional reorganisation in emerging intermittent streams. Addressing these gaps is critical for understanding how communities respond mechanistically to novel drying pressures and for improving biomonitoring tools under climate-driven regime shifts, thereby enhancing our ability to anticipate how freshwater biodiversity will reorganise under expanding flow intermittency.

Together, these frameworks lead to four mechanistic hypotheses about how flow intermittency shapes both taxonomic and functional organisation. We hypothesised (1) that local richness declines and evenness increases with drying due to environmental filtering (H1); (2) that flow intermittency reweights drying-related trait–state representation directionally and in a survival-dimension-specific manner, predicting systematic but contrasting shifts between resistance- and resilience-related states (H2); (3) that taxa possessing more drying-related trait states show greater representation under drying (H3); and finally, (4) that functional diversity and redundancy exhibit divergent ecological responses along resistance and resilience dimensions (H4).

2 | Materials and Methods

2.1 | Study Area and Sampling Design

The Bükkösdi-víz catchment, located in the Mecsek Mountains of southwest Hungary within the Pannonian ecoregion (Figure 1), has a temperate climate with sub-Mediterranean influences. We selected this catchment because it contains multiple headwater reaches that naturally differ in their degree of flow intermittency, providing an ideal natural gradient for testing how the intensity of drying affects macroinvertebrate communities. The area experiences annual mean temperatures of 10.0°C–10.2°C, more than 2000 h of sunshine, and about 760 mm of precipitation each year (Ács et al. 2015; Mezősi 2017). According to meteorological data from 1991 to 2020, seasonal averages show that summer is warm and relatively wet (21.4°C, 72.3 mm), winter is cold and dry (1.2°C, 38.7 mm), spring is moderately warm and moderately wet (11.6°C, 53 mm), and autumn brings cooling temperatures with increasing rainfall (11.6°C, 60.3 mm). Over recent decades, the region has experienced a 1.5°C increase in mean annual temperature and

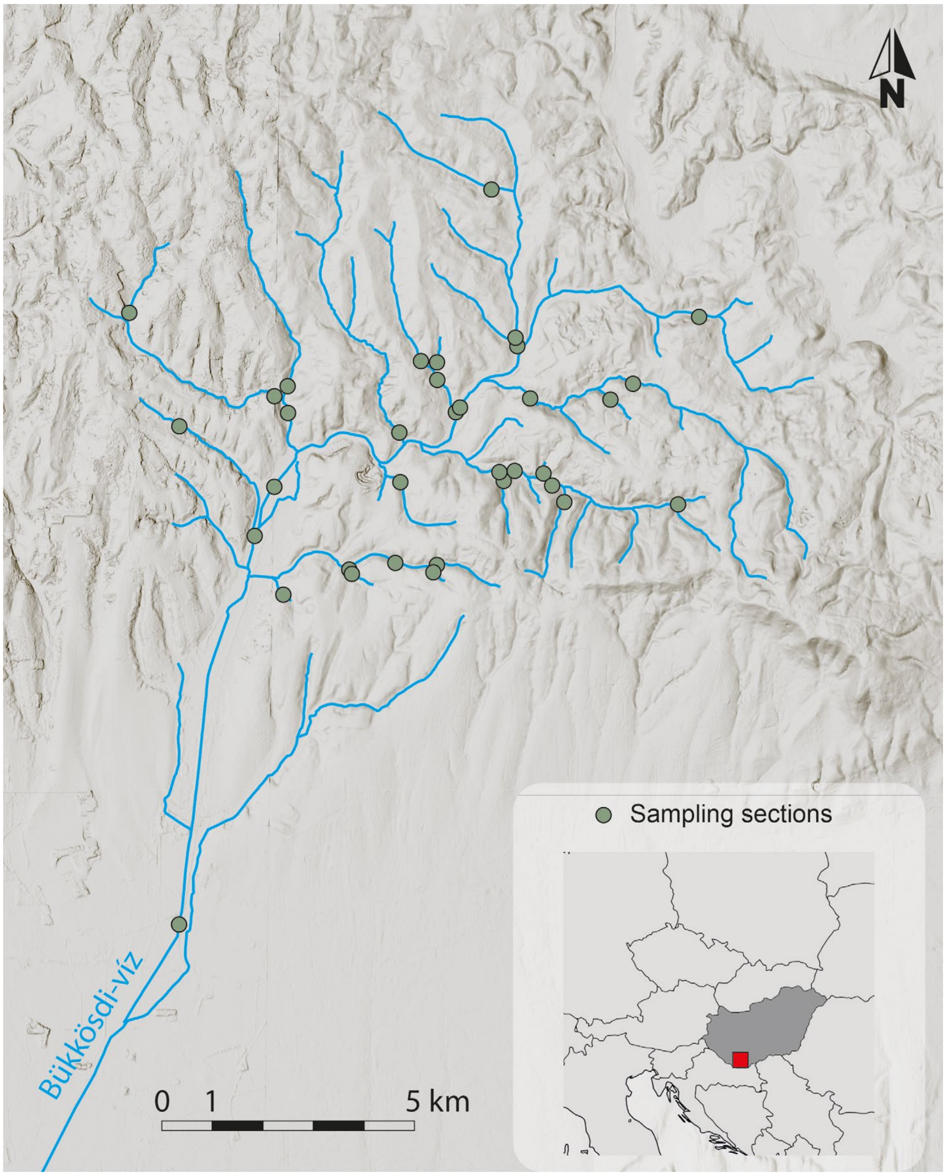

FIGURE 1 | Location of sampling reaches in the Bükkösdi-víz catchment, Mecsek Mountains, southwest Hungary. Circles indicate sampled sites, and the inset map shows the position of the catchment within Hungary.

decreasing annual precipitation, with fewer rainy days and longer dry spells, reinforcing the relevance of studying drying dynamics in this system (OMSZ 2024).

Within the catchment, stream reaches undergo seasonal transitions between flowing, non-flowing, and dry phases. These streams have coarse, bedrock-influenced substrates with minimal aquatic vegetation (typically $<5\%$ cover), and the upper reaches remain close to their near pristine state, with only minor settlements along the main channel and limited human influence. All studied streams fall under the same EU Water Framework Directive typology—calcareous watercourses of small to medium catchments at high altitudes—and therefore have similar environmental settings and a shared regional species pool. This typological consistency limits habitat-driven confounding effects and increases confidence that observed patterns primarily reflect flow intermittency.

2.2 | Macroinvertebrate Sampling

A total of 35 sampling sites were surveyed, including nine perennial sites and 26 sites with varying degrees of drying dynamics. Seasonal sampling was conducted from Autumn 2018 to Spring 2023, except for a three-season gap (Autumn 2019–Spring 2020). Sampling followed the standardised kick-and-sweep protocol using a 1-mm mesh hand net with a 0.25×0.25 m frame, covering all major mesohabitats (Boda et al. 2023). Composite samples consisted of 12 units in the first sampling year and 10 units in subsequent years. Each unit represented 0.25×0.25 m, yielding total sampled areas of $0.75\,\mathrm{m}^2$ (12-unit samples) and $0.625\,\mathrm{m}^2$ (10-unit samples), respectively. To account for differences in sampling effort, abundances were standardised to individuals per square metre. Protected species were identified in the field, recorded, and released, while all other specimens were preserved in

70% ethanol. In the laboratory, all specimens were sorted and identified to species level, except for Diptera and Turbellaria, which were identified to family level. Sampling followed national legal and ethical regulations.

2.3 | Hydrological Dataset

Hydrological conditions were continuously monitored between May 2021 and May 2023 using HOBO U20L-04 water level loggers, which recorded the presence and level of water in the streambed at each site. In addition, a 50-year dataset of daily modelled flow states was used to characterise long-term drying patterns at each site. This dataset was generated through a coupled modelling framework that combined the physically based JAMS-J2000 hydrological model (Kralisch and Krause 2006)—simulating streamflow, evapotranspiration, soil moisture, and groundwater input—with a Random Forest classification model (Breiman 2001). The Random Forest model predicted daily flow or no-flow states for each stream reach based on multiple hydro-meteorological and catchment variables, including precipitation, temperature, slope, soil type, drainage area, groundwater saturation, and historical flow data (Mimeau et al. 2024; Künne et al. 2022). From the combined HOBO and modelled flow data, we derived a Drying Degree (DD365) index, defined as the number of no-flow days during the 365 days preceding each biological sampling event. This metric provides a continuous, ecologically interpretable measure of recent drying intensity, allowing consistent comparison across sites and sampling periods. For the analysis, we used the monitored data from the period between May 2021 and May 2023. For the preceding period, we used hydrological model data (Table S1), which we slightly revised. Model estimates were scaled based on the deviations from zero of the values estimated for perennial sites. For each sampling period, we calculated the average deviation from zero of the values estimated for perennial sites, which provided the scaling factor. We corrected the model-estimated values for all sampling sites using this factor.

2.4 | Data Management

To analyse taxonomic responses (H1), we compiled a taxa × sampling-site matrix. To evaluate the functional hypotheses (H2–H4), we constructed a trait × sampling-site matrix. Due to insufficient trait coverage (< 50%), Diptera, Oligochaeta, and Turbellaria were excluded from functional analyses. Biological samples collected during the pool phases (isolated lentic pools disconnected from upstream flow) were also excluded as these represent a distinct hydrological process domain with fundamentally altered community structure (Magand et al. 2020).

Functional traits were assigned at the genus level, requiring harmonisation of records with incomplete taxonomic identification. Two situations were addressed. (1) For some families, no individuals could be reliably identified below family level, so these taxa were retained at the family level. (2) Where at least some individuals within a family were identified to genus-level (or species), the remaining family-level individuals (e.g., damaged or juvenile specimens) were proportionally distributed among the recorded genera of that family. Allocation was based on the relative abundances of genera observed during the same sampling event; if no genera were recorded for that occasion, the corresponding season for the given site was used instead. This procedure ensured consistent genus-level trait assignment without artificially inflating or deflating particular taxa.

Functional trait information was sourced from the Freshwater Information Platform (freshwaterecology.info; Schmidt-Kloiber and Hering 2015) and the DISPERSE database (Sarremejane et al. 2020). Genus-level data were used whenever available, while for a few taxa only family-level resolution was available. Where both databases provided data, the source with broader taxonomic coverage was selected to maximise consistency across taxa. We identified drying-related trait states (DRTS) and classified each as resistance-related or resilience-related based on established trait–environment relationships. Only trait states clearly linked to drying responses were included. Trait states were considered drying-related if previous studies associated them with persistence during dry phases or with post-drying recovery (Stubbington et al. 2017). In total, 15 resilience-related and 13 resistance-related trait states were retained. Traits were fuzzy-coded and standardised within each trait: each taxon's state value was divided by the sum across states for that trait, ensuring that state values per trait sum up to 1 and allowing comparability across traits and taxa.

2.5 | Data Analysis

To quantify how flow intermittency shapes taxonomic community structure (H1), we modelled changes in local richness and community evenness along the intermittency gradient. Taxonomic richness was calculated as the number of genera per sample, and community evenness was measured using Simpson diversity. Relationships with the Drying Degree (DD365) were analysed using generalised additive models (GAMs) to accommodate potential non-linear responses.

To test for directional shifts in resistance- and resilience-related trait states (H2), we calculated community-weighted means (CWMs) from genus-level relative abundances and the trait–state matrix, and modelled their relationships with DD365 using GAMs.

To identify trait states associated with persistence under drying, we applied a trait-based Community Assembly via Trait Selection (CATS) model (Warton et al. 2015). Details of the model are shown in Appendix S1. Taxon abundances were modelled using generalised linear mixed models with a negative binomial error distribution and log link. The response variable was taxon abundance, with drying intensity (DD365) as the environmental predictor and trait states included as species-level predictors. Trait–environment relationships were evaluated through interaction terms between DD365 and trait states. Species identity and sampling site were included as random intercepts to account for repeated observations and spatial structure. Positive interaction coefficients indicate trait states associated with higher abundance under increasing drying intensity, whereas negative coefficients indicate sensitivity to drying. Model fit and diagnostics (residual structure, dispersion, and zero inflation) were verified to ensure robustness. Models were fitted using the glmmTMB package in R, and model diagnostics were examined to verify dispersion and residual structure.

To test whether taxa with more drying-related trait states perform better under drying (H3), we calculated for each taxon an R-factor, defined as the total number of DRTS possessed (Figure 2). Trait states showing positive relationships with DD365 in the CATS analysis were included, regardless of individual significance, as they represent functionally relevant responses. Rare taxa, defined as those occurring in fewer than 5 sampling events, were excluded, leaving 61 taxa. Analyses were performed for all DRTS combined (RF), and separately for resilience-related (RL) and resistance-related (RT) states. RL and RT are not mutually exclusive; the same taxon may express states from both dimensions, and their sum defines the overall R-factor (RF). We then examined how the proportion and relative abundance of taxa in each RF class changed along the intermittency gradient using GAMs.

To evaluate functional restructuring (H4), we quantified functional richness (FRic), Rao's quadratic entropy (RaoQ), and functional redundancy (FRed) separately for resilience- and resistance-related trait states. FRic and RaoQ were calculated from genus-level trait data using Gower dissimilarities, and FRed was derived from taxon–trait overlap metrics. For comparison, and as required for calculating FRed we also calculated genus richness and Simpson diversity. All analyses were performed in R version 4.4 (R Core Team 2024) using standard packages for functional diversity and modelling, including mgcv (Wood 2024), FD (Laliberté et al. 2014), glmmTMB (Brooks et al. 2017), and the tidyverse suite (Wickham et al. 2019).

3 | Results

3.1 | Taxonomic Composition of Macroinvertebrate Assemblages

A total of 680,782 individuals, representing 124 genus- or family-level taxa were recorded. The assemblage comprised 12 Gastropoda, 2 Bivalvia, 4 Hirudinea, 5 Crustacea, 12 Ephemeroptera, 11 Odonata, 5 Plecoptera, 11 Heteroptera, 38 Coleoptera, 1 Megaloptera, and 23 Trichoptera taxa. Crustaceans dominated numerically, accounting for more than half of all individuals (361,389). Taxonomic richness declined significantly with increasing DD365, whereas Simpson diversity increased (Figure 3). These patterns correspond to the expectations of H1, which predicted decreasing richness and increasing evenness along the intermittency gradient.

3.2 | Changes in Drying-Related Trait States

Trait–environment relationships revealed dimension-specific responses of drying-related trait states (Table 1). Among the 15 resilience-related states, most showed negative or weak associations with flow intermittency, whereas six displayed

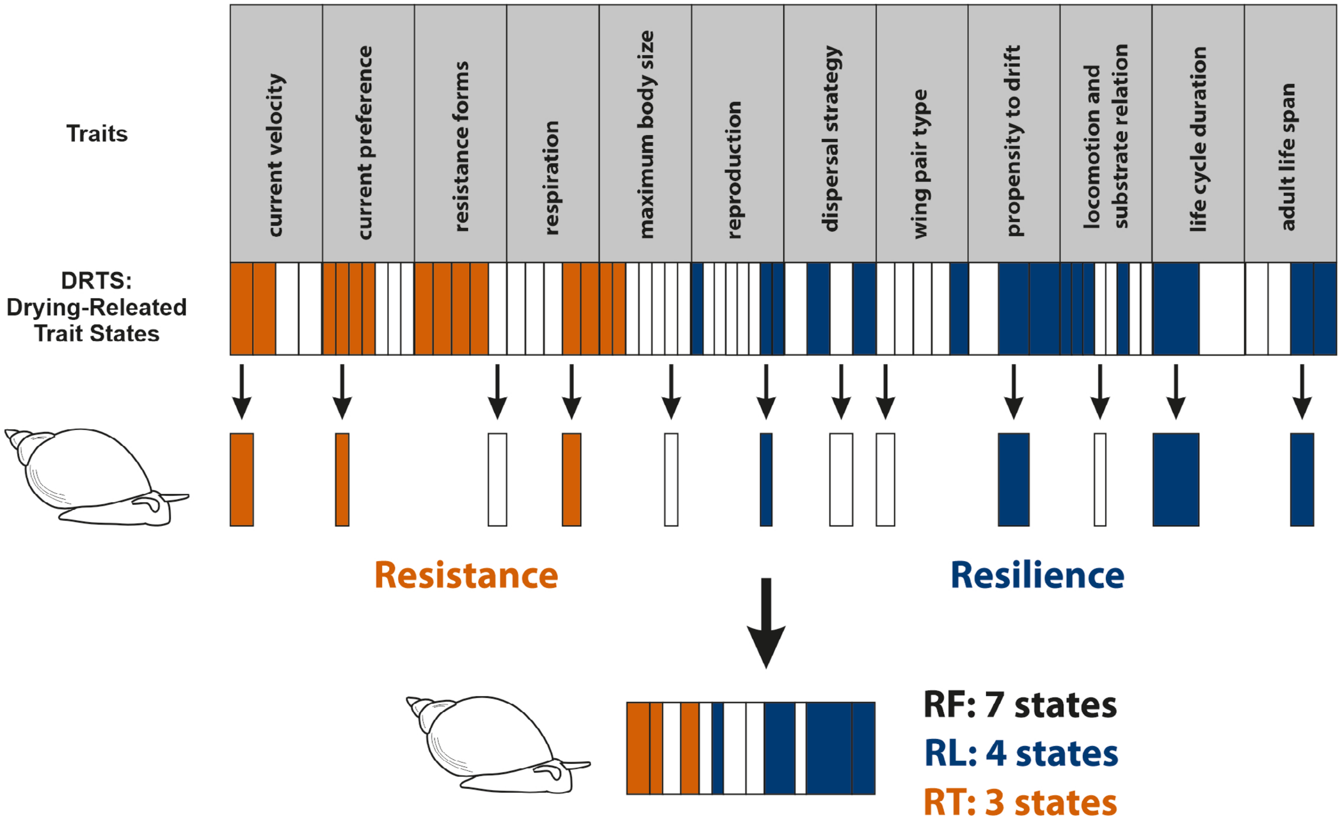

FIGURE 2 | Schematic illustration of the counting procedure for resilience (RL) and resistance (RT) trait states and their sum, the overall R-factor (RF). Each taxon contributes to both RL and RT classes, which are not mutually exclusive (e.g., a taxon with RL 3 and RT 4 is counted as RF 7).

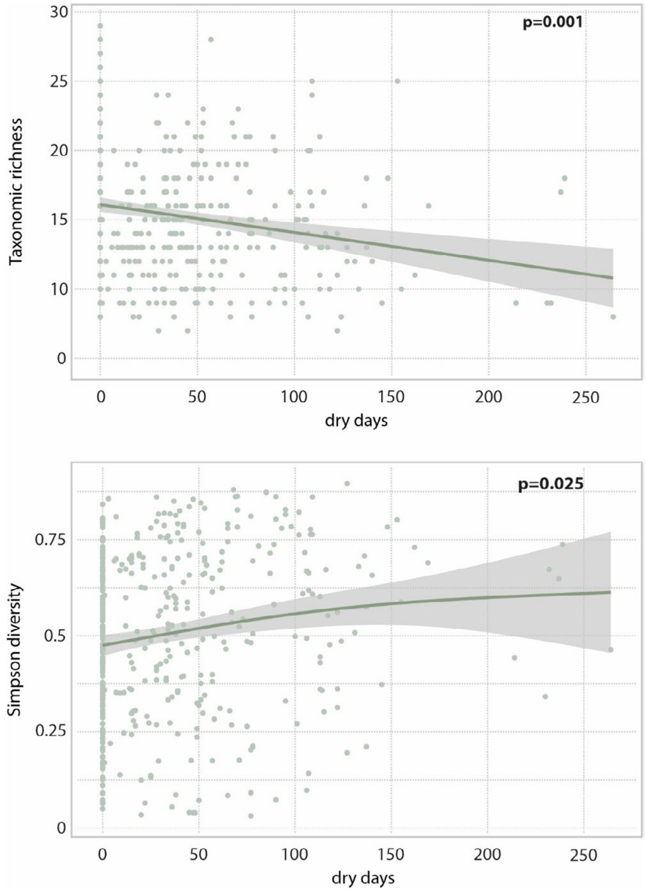

FIGURE 3 | Responses of taxonomic richness and Simpson diversity to increasing flow intermittency (Drying Degree, DD365). Lines represent fitted generalised additive model (GAM) trends with 95% confidence intervals.

positive responses. In contrast, 10 of the 12 resistance-related states showed positive coefficients and two exhibited negative trends. Among resistance-related states, most trends were positive, whereas resilience-related states showed a mixture of positive and negative responses. Coefficient magnitudes ranged between −0.5 and +0.6, with approximately half of the trait states showing significant ($p < 0.05$) responses to flow intermittency. These patterns relate to H2, which predicted dimension-specific shifts in drying-related trait states along the intermittency gradient.

3.3 | Co-Occurrence of Trait States

Pairwise analyses showed no strictly co-occurring drying-related traitstates pairs (i.e., no combinations were universally present or absent together across taxa). Several trait–state combinations exhibited significant positive correlations (Spearman's $\rho = 0.57$–0.90; Table 2). The strongest associations occurred within resilience-related traits (e.g., wing morphology and flying ability), while moderate links were detected between resilience and resistance dimensions (e.g., flying ability and aerial respiration). These correlations indicate that some trait–state pairs frequently co-occur, whereas no pairs showed strictly deterministic co-occurrence across taxa.

3.4 | Quantitative Analysis of Drying-Related Trait States

In total, 16 drying-related trait states (DRTS) showed positive associations with the intermittency gradient in the CATS analysis and were therefore included in the R-factor (RF) calculation (See Table 1). Across taxa, the number of DRTS ranged from 0 to 9 (Table 3). Within dimensions, up to five resilience-related (RL) and five resistance-related (RT) states were observed. Because taxa can express states from both dimensions, RL and RT categories overlap, and their sum determines the overall RF. The number of taxa and individuals (ind m^{-2}) in each R-factor class is shown in Table 3.

3.4.1 | Overall R-Factor

R-factor (RF) values were concentrated around intermediate classes under perennial conditions, with RF5 dominating. As DD365 increased, the representation of RF5 decreased, while RF2 and RF7 increased (Figure 4a). RF1 and RF8–RF9 remained consistently rare across the gradient. Abundance-based patterns (Figure 4b) were similar: RF5 dominated under low intermittency but decreased toward higher DD365, whereas RF7 increased at higher DD365.

3.4.2 | Resilience-Related States (RL)

RL2–RL4 dominated under perennial flow. RL2 declined with increasing DD365, and RL3 peaked mid-gradient before decreasing (Figure 4c). RL0 increased toward higher DD365, indicating simplified resilience portfolios. Abundance-based patterns matched these trends (Figure 4d).

3.4.3 | Resistance-Related States (RT)

RT0–RT3 dominated under perennial conditions. RT1 increased with DD365, RT2 and RT3 showed mid-gradient shifts, and RT4–RT5 remained minor contributors (Figure 4e). Abundance-based patterns were similar (Figure 4f).

Statistical details for all GAM trends are provided in Table S2. These patterns align with H3, which expected systematic changes in the distribution of RF classes along the intermittency gradient.

3.5 | Functional Diversity Analysis

Functional diversity showed clear dimension-specific responses to intermittency (Figure 5a–f). For resilience-related trait states, functional richness (FRic) and Rao's quadratic entropy (RaoQ) both declined significantly (Figure 5a,b), while functional redundancy (FRed) showed no significant trend (Figure 5c). For resistance-related trait states, FRic showed no significant change (Figure 5d), RaoQ displayed a slight but non-significant increase at low intermittency (Figure 5e), and functional redundancy declined significantly (Figure 5f). These results correspond to H4, which anticipated dimension-specific responses in functional richness, redundancy, and Rao's quadratic entropy.

TABLE 1 | Results of trait-by-environment models assessing the effect of flow intermittency (number of dry days) on drying-related trait states (DRTS). Columns show model estimates (β), standard errors (SE), p-values, and the direction of the association with intermittency ('positive' = higher representation; 'negative' = lower representation). Trait states are classified as resistance- or resilience-related.

	Trait	Trait state	Estimate (β)	Standard error (SE)	p	Direction
Resilience	Adult life span	≥ 1 year	−0.0132	0.0031	0.0000	Decrease
	Adult life span	1 month—1 year	0.0034	0.0015	0.0234	Increase
	Dispersal strategy	Aerial active	−0.0013	0.0032	0.6936	Decrease
	Dispersal strategy	Aquatic active	0.0150	0.0047	0.0013	Increase
	Life cycle duration	≤ 1 year	−0.0026	0.0017	0.1377	Decrease
	Locomotion and substrate relation	Flier	0.0029	0.0157	0.8552	Increase
	Locomotion and substrate relation	Full water swimmer	−0.0057	0.0034	0.0975	Decrease
	Locomotion and substrate relation	Interstitial (endobenthic)	−0.0173	0.0121	0.1517	Decrease
	Locomotion and substrate relation	Surface swimmer	−0.0178	0.0081	0.0285	Decrease
	Propensity to drift	Frequent	−0.0028	0.0039	0.4750	Decrease
	Propensity to drift	Occasional	0.0059	0.0028	0.0318	Increase
	Reproduction	Clutches, terrestrial	0.0002	0.0043	0.9682	Increase
	Reproduction	Ovoviviparity	0.0019	0.0024	0.4283	Increase
	Wing pair type	1 pair +1 pair of elytra/hemielytra	−0.0014	0.0028	0.6099	Decrease
	Wing pair type	2 similar-sized pairs	−0.0032	0.0020	0.1015	Decrease
Resistance	Current preference	Limno- to rheophi	0.0037	0.0017	0.0293	Increase
	Current preference	Limnobiont	0.0069	0.0021	0.0008	Increase
	Current preference	Limnophil	0.0003	0.0027	0.9239	Increase
	Current velocity	Null	0.0006	0.0033	0.8614	Increase
	Current velocity	Slow	−0.0020	0.0023	0.3786	Decrease
	Maximum body size	< 0.25	0.0483	0.0218	0.0268	Increase
	Maximum body size	0.25–0.5	−0.0075	0.0022	0.0007	Decrease
	Resistance forms	Cocoons	0.0077	0.0066	0.2479	Increase
	Resistance forms	Diapause or dormancy	0.0053	0.0019	0.0052	Increase
	Resistance forms	Eggs, gemmula, statoblasts	0.0015	0.0024	0.5396	Increase
	Resistance forms	Housings against desiccation	1.1137	4.5496	0.8066	Increase
	Respiration according to Tachet	Spiracle (aerial)	0.0010	0.0034	0.7704	Increase

4 | Discussion

4.1 | Community/Assemblage Reorganisation Under Flow Intermittency

Assemblages in newly intermittent streams underwent clear reorganisation along the intermittency gradient. Environmental filtering reduced local richness, redistributed abundances, and was associated with selective rather than uniform shifts in functional composition. Only a subset of drying-related trait states increased in representation, and functional distributions differed between resilience- and resistance-related dimensions. Together, these changes indicate that community assembly in transitional DRNs is influenced by selective

TABLE 2 | Pairwise correlations among drying-related trait states (DRTS) across taxa. Only positive and significant ($p < 0.05$) correlations are included.

Trait state 1		**Trait state 2**			
Name of the trait state 1	**Related strategy dimensions**	**Name of the trait state 2**	**Related strategy dimensions**	**Spearman_rho**	***p***
Wing pair type—1 pair +1 pair of elytra/hemielytra	Resilience	Locomotion and substrate relation—flier	Resilience	0.895	<0.001
Wing pair type—1 pair +1 pair of elytra/hemielytra	Resilience	Respiration—spiracle (aerial)	Resistance	0.712	<0.001
Propensity to drift—Occasional	Resilience	Propensity to drift—Frequent	Resilience	0.568	<0.001
Locomotion and substrate relation—flier	Resilience	Respiration—spiracle (aerial)	Resistance	0.69	<0.001

TABLE 3 | Distribution of taxa and individuals across R-factor (RF) classes, defined as the number of drying-related trait states (DRTS) expressed per taxon. Values are given separately for all DRTS combined, resilience-related (RL), and resistance-related (RT) states, with the number of taxa and standardised abundances (individuals m^{-2}) for each class.

	DRTS		**Resilience-related trait states (RL)**		**Resistance-related trait states (RT)**	
R-factor (RF)	**No. of taxa**	**ind/m^2**	**No. of taxa**	**ind/m^2**	**No. of taxa**	**ind/m^2**
0	10	11,724.8	10	11,724.8	40	233,366.8
1	6	2489.1	13	3379.4	23	549,241.2
2	23	198,783.7	56	287,985.9	22	63,010.7
3	21	31,785.9	34	171,495.4	27	167,546.0
4	13	41,684.6	9	539,621.9	9	756.3
5	22	596,186.9	2	736.5	3	1022.9
6	14	129,343.9				
7	11	1185.6				
8	2	1236.8				
9	2	522.7				

functional filtering—the quality rather than the quantity of trait combinations—and by asymmetric responses of resistance and resilience attributes. Similar patterns of richness loss, abundance redistribution, and dimension-specific trait adjustments have been documented across diverse intermittent systems, underscoring that early-stage drying consistently favours selective functional reorganisation rather than uniform shifts (Boersma et al. 2014; Datry et al. 2014; Stubbington et al. 2017).

4.2 | Taxonomic Responses (H1)

Flow intermittency acted as a strong environmental filter, resulting in declining richness and increasing evenness with rising DD365 (Figure 3). These findings are consistent with global patterns of taxon loss in intermittent systems (Crabot et al. 2021; Datry et al. 2014). The concurrent increase in evenness, derived from Simpson diversity results, indicates that filtering redistributes relative abundances, not only reduces richness, highlighting a restructuring of dominance patterns. Although evenness responses are inconsistently reported in the literature (Chanut et al. 2023; Leigh, Boulton, et al. 2016), our findings show that newly intermittent systems can exhibit increased evenness, consistent with early-stage shifts in community organisation during transition to intermittency.

4.3 | Trait–State Filtering (H2)

Trait–environment models revealed dimension-specific filtering, with most resistance-related states showing positive associations with intermittency and resilience-related states showing a mixture of negative and positive relationships (Table 1). This selective filtering indicates that environmental constraints in newly drying systems act on individual

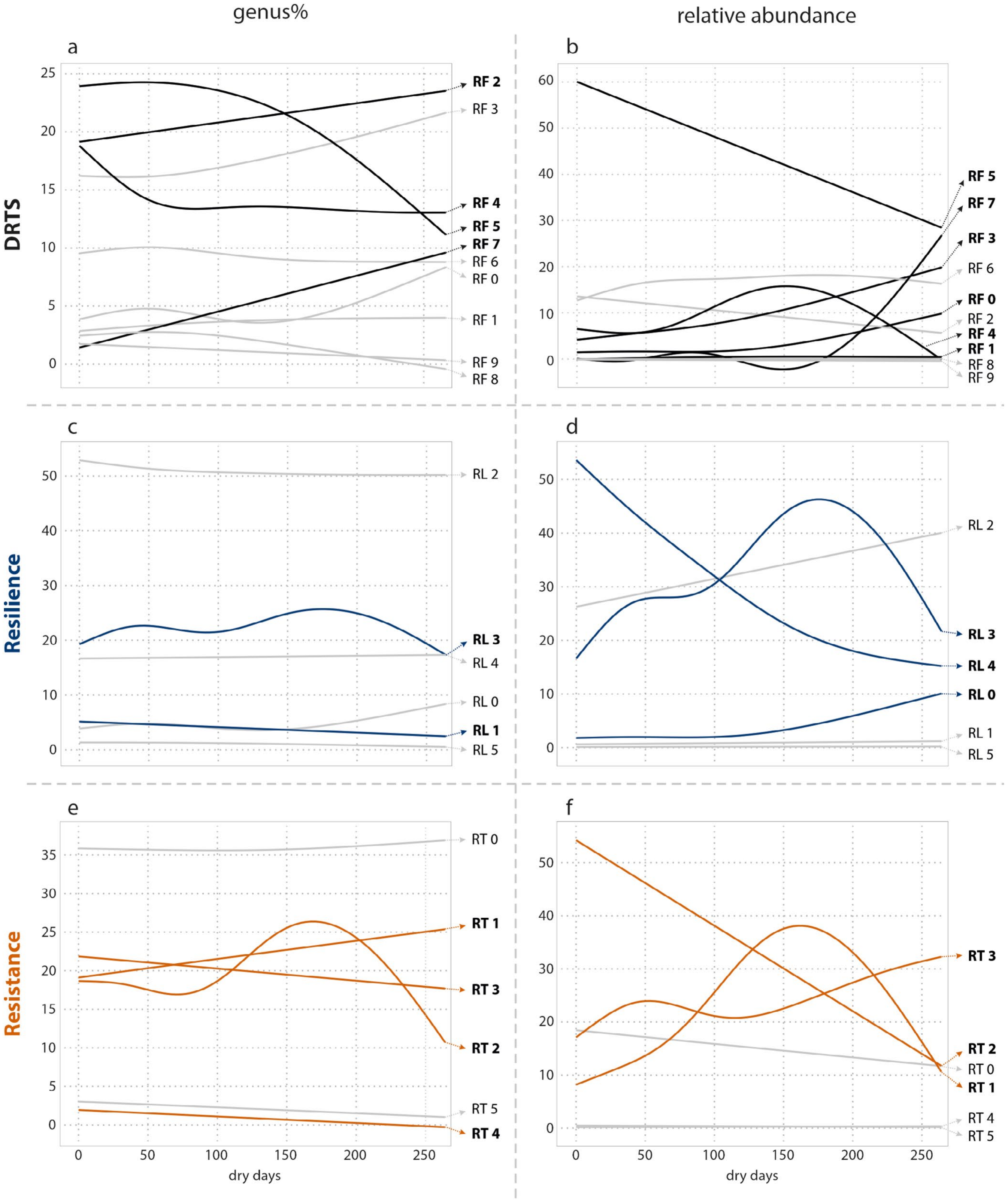

FIGURE 4 | Responses of the R-factor (RF; number of drying-related trait states, DRTS, per taxon) to increasing flow intermittency. Panels show how the proportion of the total community represented by each RF class changes along the intermittency gradient (x-axis = dry days). The left column (a, c, e) shows the *proportion of genera* (genus %), and the right column (b, d, f) shows the *proportion of total relative abundance* contributed by each class. Separate panel rows illustrate overall RF classes (0–9), resilience-related classes (RL 0–5), and resistance-related classes (RT 0–5). Lines represent fitted trends.

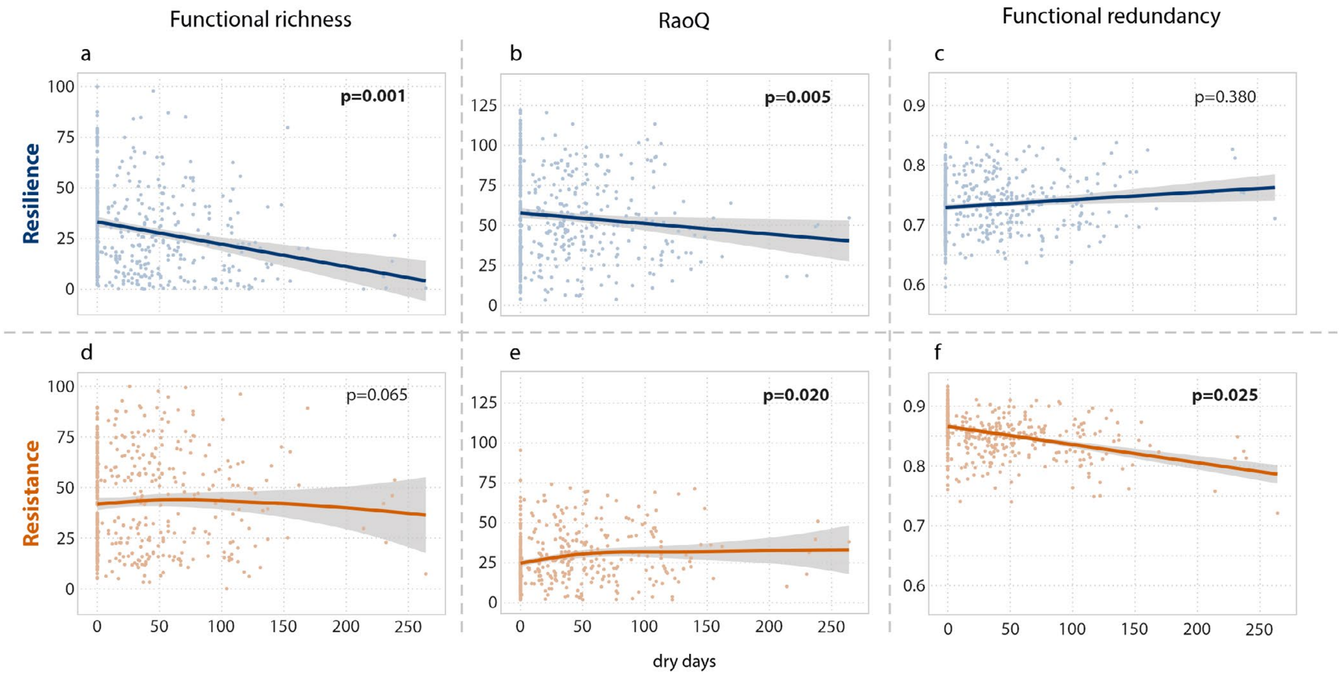

FIGURE 5 | Responses of functional diversity metrics to increasing flow intermittency. Panels display functional richness (FRic), Rao's quadratic entropy (RaoQ), and functional redundancy (FRed) for resilience-related (top row) and resistance-related (bottom row) trait states, with lines representing fitted GAM trends and 95% confidence intervals; *p*-values correspond to the significance of the smoothing term.

trait states rather than uniformly across entire survival dimensions. Several resistance-related states such as dormancy and protective forms became more prevalent, whereas others remained unchanged, and resilience-related states showed similarly mixed responses. Previous studies often emphasised the dominance of resistance traits in transitional streams (e.g., Bozóki et al. 2024; Leigh, Bonada, et al. 2016; Vander Vorste et al. 2016); our results refine this common assumption by demonstrating that drying strengthens particular trait states rather than entire trait dimensions. This pattern indicates that drying reorganises functional composition through heterogeneous state-level responses rather than coherent dimension-wide shifts.

4.4 | Cumulative Advantage and Trade-Offs (H3)

Taxon performance along the intermittency gradient did not increase monotonically with the number of drying-related trait states (Figure 4). Although taxa with several DRTS were present across the gradient, intermediate RF classes were more frequently represented under stronger intermittency than the highest classes. High RF classes remained rare and did not expand with increasing intermittency, and some classes showed stable, low representation across the gradient. Similar stabilisation of trait combinations has been reported elsewhere, with trait composition proving more persistent than taxonomic composition across environmental gradients (Gallardo et al. 2014; Roux and Clinton 2023). These patterns indicate that stable classes in our data reflect genuine, persistent strategies rather than sampling artefacts. These patterns do not support a simple cumulative-advantage expectation, as increases in DRTS did not correspond to a monotonic increase in representation along the gradient. This likely reflects basic ecological constraints: several drying-related trait states incur costs or conflict functionally with one another, limiting the feasibility of highly stacked portfolios (Northfield et al. 2021). As a result, only a restricted set of internally coherent trait–state combinations remains viable under emerging intermittency. Instead, ecological costs, trade-offs and incompatibilities among particular trait states likely limit multifunctionality. Because RL and RT classes represent dimension-specific profiles within the same assemblages, our results show that the configuration and ecological coherence of trait–state portfolios matter more than their total number—pointing toward the importance of particular rather than cumulative trait–state combinations under drying.

4.5 | Functional Divergence (H4)

Functional diversity analyses revealed asymmetric responses between resilience- and resistance-related trait dimensions (Figure 5). On the resilience dimension, functional richness and Rao's quadratic entropy declined while redundancy remained low, consistent with fewer resilience-related combinations contributing to functional structure under stronger drying. On the resistance dimension, functional space was maintained or slightly expanded, yet redundancy decreased, suggesting that multiple persistence strategies persisted but with reduced buffering capacity. Comparable asymmetries have been documented in long-established intermittent systems (Crabot et al. 2021; Leigh, Bonada, et al. 2016), and our findings show that such imbalances can emerge early during the transition to intermittency. Because resistance and resilience attributes originate from the same taxa, the divergence reflects reweighting of functional attributes within shared assemblages rather than replacement between distinct taxonomic groups. Ecologically, this asymmetry suggests that drying may constrain resilience-related attributes earlier, while resistance-related attributes remain more diverse but show reduced redundancy, potentially leaving assemblages vulnerable in different ways along the two survival dimensions.

4.6 | Implications for Assessment and Monitoring

Flow intermittency is a hydrological regime rather than a classical anthropogenic pressure, yet current bioassessment frameworks—such as those aligned with the Water Framework Directive—were designed for perennial systems and calibrated against pressure gradients like nutrient enrichment or morphological alteration. Applying these frameworks to intermittent streams risks misclassification because ecological responses to drying differ in both form and mechanism. Our findings show that, although diagnostic, the decline of richness is still insufficient as a single metric, whereas evenness can increase under filtering, complicating the interpretation of standard diversity metrics. Functional reorganisation was most evident at the trait–state level, where selective filtering and optimal combinations emerged as key signals. Trait–state metrics detect functional erosion earlier than taxonomic indicators, making them particularly valuable for identifying early-stage ecological vulnerability in drying streams. These findings indicate that intermittency-aware indices could benefit from integrating trait–state information and redundancy metrics to capture functional vulnerability at an early stage. Incorporating such indicators into monitoring could improve evaluation of ecological status under climate-driven drying regimes.

4.7 | Limitations and Future Directions

Limitations include the absence of explicit connectivity metrics, which restricts interpretation of resilience pathways, and the lack of multi-year seasonal dynamics. Trait–state assignments, while robust, involve uncertainty. Some RF classes remained small, which may have limited statistical power, although patterns were consistent across richness- and abundance-based analyses. Future work should quantify hydrological connectivity, incorporate multi-year dynamics, and examine trait–state configurations rather than counts alone. Comparisons between newly and historically intermittent systems will help disentangle transitional responses from long-term equilibria.

5 | Conclusion

Flow intermittency in newly intermittent streams reshapes macroinvertebrate assemblages through selective functional filtering, optimal rather than cumulative trait–state portfolios, and divergent functional responses of resistance and resilience dimensions. Assembly responses in transitional DRNs are thus structured by selective mechanisms rather than uniform shifts, with direct implications for bioassessment under climate-driven drying. Differences between resistance and resilience responses reflect within-taxon reweighting of functional attributes, highlighting early-stage functional vulnerability in DRNs. These insights highlight the importance of mechanistic trait–state perspectives for forecasting ecosystem responses under global freshwater drying.

Author Contributions

Tamás Bozóki: conceptualization (equal), data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), visualization (equal), writing – original draft (equal), writing – review and editing (equal). **Zoltán Csabai:** conceptualization (equal), writing – review and editing (equal). **Márk Ficsór:** formal analysis (equal), writing – review and editing (equal). **Júlia Szeles:** data curation (equal), formal analysis (equal), investigation (equal), writing – review and editing (equal). **Gábor Várbíró:** formal analysis (equal), methodology (equal), writing – review and editing (equal). **Pál Boda:** conceptualization (equal), data curation (equal), funding acquisition (equal), investigation (equal), methodology (equal), resources (equal), supervision (equal), writing – original draft (equal), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in this study are publicly available in https://zenodo.org/records/17776384.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ece373365-sup-0001-Supinfo01.docx. **Table S1:** Hydrological data for sampling sites (number of dry days in the 365 days preceding sampling) as sampling site × sampling occasion. The colour gradient fill of cells indicates the degree of drying, dark blue—perennial, orange—high degree of drying. **Table S2:** p-values for GAM models testing changes in the proportional representation of R-factor (RF), resilience-related (RL), and resistance-related (RT) classes along the intermittency gradient. Values are provided separately for genus-level proportions (genus %) and relative abundance (rel. ab.). Significant effects ($p < 0.05$) are shown in bold.