



Exploring macroinvertebrate community assembly rules: unraveling the effects of flow intermittency and poor ecological potential on environmental filtering and limiting similarity through functional traits

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Abstract Flow intermittency and poor environmental conditions can occur separately or simultaneously, affecting the occurrence of trait states in stream macroinvertebrate assemblages. Within the framework of limiting similarity theory, we investigate whether environmental filtering or limiting similarity serves as the primary driver force under three environmental conditions: unstressed (perennial environment and good ecological potential), single-stressed (intermittent condition or poor ecological potential), and multi-stressed (intermittent condition and poor ecological potential) environments. Our analysis validated neutral trait states that are not influenced by

different environmental stressors. In unstressed environments, limiting similarity is the primary driver force shaping the macroinvertebrate community. In stressed environments, however, the type of stress determines the influence of environmental filtering. It is not the quantity but rather the quality of stress that increases the influence of environmental filtering. Flow intermittency has a more pronounced effect on the aquatic community than poor ecological potential because it eliminates living conditions, while poor ecological conditions merely restrict them. As anticipated, we observed that certain trait states have specific responses indicating that different driver forces influence them across various environmental conditions. Our study provides valuable insights for managing freshwater habitats and developing adaptive conservation strategies considering increasing drought frequency worldwide.

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Introduction

Understanding the major processes that shape local communities is a central issue of community ecology (Keddy, 1992). Community composition at a given site is controlled by abiotic and biotic factors that function as a series of filters (Weiher & Keddy, 2001; Leibold & McPeck, 2006). These filters do not select species directly but instead favor certain traits, allowing only organisms with the appropriate trait characteristics to persist. For aquatic macroinvertebrates, traits refer to morphological, physiological, behavioral, and life-history characteristics that shape their ecological roles and responses to environmental factors. These traits determine how species interact with each other, respond to environmental conditions, and contribute to ecosystem processes. Each trait (e.g. life cycle duration) consists of multiple trait states (i.e. trait categories or trait modalities) (e.g. ≤ 1 year or > 1 year), which describe the different possible expressions of that trait. Individuals of a species can possess one trait state from each trait (Usseglio-Polatera et al., 2000), and together these form a unique trait state complex for the species. In the context of flow intermittency, we illustrate the trait state complex through two examples of traits: body size and wing size. Body size plays a key role in an organism's survival strategy, as species with smaller body sizes are better adapted to avoid flow intermittency by easily reaching hyporheic zones. In contrast, larger wings represent better dispersal abilities, allowing populations to recover more quickly after disturbances through aerial dispersal (Datry et al., 2017). These different trait states can exist in various combinations and this approach can be generalized to another trait states. For instance, some organisms may be small but lack wings (e.g. small crustaceans), others may have large bodies and large wings (e.g. diving beetles), while others may be larger-bodied but wingless (e.g. larger leaches).

Community assembly theory suggests that species composition is the deterministic outcome of major processes such as dispersal limitation, biotic interactions and environmental suitability (Weiher et al.,

2011). In freshwater ecosystems, particularly among aquatic macroinvertebrates, the lack of geographical barriers, small spatial scale, and relatively high dispersal capacity often minimize the influence of spatial limitation (Schmera et al., 2018; Cunillera-Montcusí et al., 2020). Consequently, two distinct, non-random processes of species sorting exist. First, environmental filtering strongly determines which species from the regional species pool can survive and reproduce in specific habitats (Menge & Olson, 1990; Ricklefs & Schluther, 1993; Elliot et al., 1995; Poff, 1997). A species can persist locally if its trait state complex aligns with habitat conditions and enables adaptation to local biotic interactions (Karr, 1991; Mackay, 1992; Sweeney, 1993; Townsend et al., 1997). Species lacking appropriate traits or trait combinations are filtered out by environment (Poff, 1997; Götzenberger et al., 2012). Furthermore, environmental filtering causes trait convergence, where species within a community exhibit similar trait states more frequently than expected by random chance (Grime, 2006; Laliberté et al., 2013). In contrast, limiting similarity (MacArthur & Levins, 1967) results in the opposite trait state patterns and leads to trait divergence. This theory suggests that species experience less competition when their niches differ, resulting in stable coexistence (MacArthur & Levins, 1967; Meszéna et al., 2006). Divergent trait states reduce competition for resources, meaning species within a community are more different than expected by random selection (MacArthur & Levins, 1967; Meszéna et al., 2006).

These two non-random processes—environmental filtering and limiting similarity—shape the functional trait states within communities in different ways. This provides a useful and widely used framework for testing community assembly rules along environmental gradients (Cornwell & Ackerly, 2009; Götzenberger et al., 2012; Botta-Dukát & Czúcz, 2016). In habitats with increased environmental stress, environmental filtering is the dominant process, while limiting similarity becomes dominant under more favorable conditions (Ács et al., 2019). All in all, this theory allows for the examination of community composition from both structural and functional perspectives. It provides a valuable framework for understanding the dynamics that determine species coexistence, trait divergence, and community assembly across varying environmental gradients. By considering both the

competitive forces (hereafter driver forces) associated with limiting similarity and the selective pressures of environmental filtering, we can gain deeper insights into how ecological communities are structured and how species adapt to different environmental conditions (Ge et al., 2021).

Freshwaters are among the most diverse ecosystems; however, they are threatened by the effects of global warming and human activities, which among other things, modify the quantity and quality of the water (Allan, 2004; Dudgeon et al., 2006; Reid et al., 2019). Climate change and an increase in anthropogenic water abstraction (IPCC, 2007; Kernan et al., 2011; IPCC, 2014) have a key effect on water quantity resulting in a shift of perennial watercourses becoming intermittent (Döll & Schmied, 2012; Tölle et al., 2018; B-Béres et al., 2019). Hereafter, surface waters are considered intermittent (Busch et al., 2020) if they do not have a constant flow or presence of water throughout the year and their hydrological phases alternate between wet and dry periods. The flow intermittency generates extreme conditions that might become one of the strongest environmental pressures that aquatic communities would face and must adapt to. Organisms in perennial streams typically prefer steady and constant flow, while in intermittent streams the species aggregate from assemblages in the flowing, ponded or even dry phases (Stubbington et al., 2017). Intermittency can lead to compositional changes as a consequence of the appearance of sensitive taxa (Boulton, 2003). At a local scale, the continuous and cyclical changes in hydrological phases can result in lower species richness in intermittent streams compared to perennial streams (Boulton & Lake, 2008; Lake, 2011; Soria et al., 2017). Compositional changes in the community along hydrological regimes over time (known as ‘time-sharing’) due to increased habitat heterogeneity (Dieterich & Anderson, 2000) can often lead to an increase in both alpha and beta diversity (Bogan et al., 2015; Stubbington et al., 2017) compared to perennial systems, even though flow intermittency acts as a strong environmental filter (McGill et al., 2006; Díaz et al., 2007).

In addition, anthropogenic disturbances such as land use (Wang et al., 1997), sewage inflow (Nelson, 2011), and streambed modification (Cooper, 1993; Beisel et al., 2000) have a substantial (indirect or direct) effect on species composition via water quality. The quality of habitat has a significant impact on

the macroinvertebrate’ composition and abundance (Heatherly et al., 2007). Habitats of higher quality with minimal anthropogenic disturbance and lower nutrient concentrations maintain greater richness and diversity of macroinvertebrates, as well as a higher number of sensitive species (Heatherly et al., 2007). As water quality deteriorates, there is a decrease in the abundance of the most quality-sensitive taxa (Barbour et al., 1992; Stewart et al., 2001; Wilkins et al., 2015). Decreasing water quality or shortage in water quantity tends to generate changes in aquatic communities per se, but they might have a synergistic effect if they act simultaneously. Thus, the flow intermittency and poor environmental conditions of aquatic habitats also pose significant threats to habitat diversity. Habitat diversity loss caused by flow intermittency significantly reduces the availability of viable areas, presenting a major challenge for species distribution and maintenance (Dudgeon et al., 2006). Organisms may become isolated, reducing genetic flow between species and increasing the risk of extinction for small populations (Kolasa & Pickett, 1991). The deterioration of water quality caused by heavy metals and chemical pollutants also reduces ecosystem stability and species interactions in the long term (Carpenter et al., 1998). Excessive nutrient input from agricultural sources leads to algal blooms, which suppress aquatic plants. Taken together, declines in water quality and increases in flow intermittency have severely reduced the extent and complexity of unique habitats, thereby endangering the survival of endemic species (Davis et al., 2005). These environmental changes also have indirect effects on wildlife. The reduction of habitats and the decline in water quality led to the shrinkage of populations of many freshwater species, contributing to a global decline in biodiversity in the long term (Woodward et al., 2012). Such changes can also alter the structure and function of food webs, thereby weakening ecosystem resilience and stability.

In brief, hydrological regimes and water quality can individually and interactively determine community composition from the same species pool (Karr, 1991; Mackay, 1992; Sweeney, 1993; Wallace & Webster, 1996; Townsend et al., 1997). Flow intermittency and poor ecological conditions, as stressors, may occur either separately or simultaneously across different streams (Lukács et al., 2021). The EU-WFD concept uses the term “ecological potential” to assess and manage heavily modified and artificial

water bodies similar to the term “ecological quality” used in natural waterbodies. Within the scope of the EU Water Framework Directive (WFD) assessment in Hungary, a total of 886 water bodies were evaluated. Among these, 55% were identified as intermittent, with the majority situated in lowland areas. Notably, the watershed of these intermittent water bodies is predominantly characterized by agricultural land use, which is the primary economic activity in the regions (Carpenter et al., 1998; Moss, 2007). Considering the diverse ecological states of these streams and the increasing frequency of drying due to climate change, they provide an excellent subject for investigating the effects of a multi-stress environment on the macroinvertebrate community, utilizing the theoretical framework as previously mentioned. The interplay between limiting similarity and environmental filtering, as the two main drivers of community structure, depends on both the trait states possessed by the species and the environmental conditions they inhabit. To reveal this, we tested the probability of the presence of trait states, focusing on which driver forces (environmental filtering which leads to trait convergence or limiting similarity which leads to trait divergence) have an effect on the different trait states. The study was conducted on invertebrate assemblages under four different environmental conditions: unstressed (perennial environment and good ecological potential), single-stressed (intermittent environment or poor ecological potential), and multi-stressed environments (intermittent environment and poor ecological potential).

Our study aimed to determine whether environmental filtering or limiting similarity is the primary driver force in the trait states of the lowland aquatic macroinvertebrate community in different stress levels. In this study, we sampled streams across Hungary to evaluate the following hypotheses:

- (i) Certain trait states are neutral across a wide range of environmental conditions, meaning they occur in unstressed, single-stressed and multi-stressed conditions. These neutral trait states can facilitate species coexistence through limiting similarity, where species with similar trait states can coexist by occupying slightly different niches within the same environment. Based on this, we assume that neutral trait states are likely to be associated with limiting similarity under various pressures.

- (ii) In general, environmental filtering dominates stressful environments by selecting for certain trait states, while limiting similarity becomes more relevant in stable environments where species interactions (like competition) drive community composition. Thus, we hypothesized that in multi- or single-stressed environments, environmental filtering will be the primary driver of community assembly, while limiting similarity will become dominant under unstressed environmental conditions. We presume that the primary driver force for the whole community is the one whose impact is detectable in a greater number of trait states.
- (iii) Some trait states may be more relevant in specific environmental conditions. We assumed that these relevant trait states are specific for either unstressed, single- or multi-stressed environments and they can be detected.

Materials and methods

Study area

The studied streams are found in the Pannonian Basin of Hungary, a plain which is surrounded by mountains that create a specific climate influencing the region's biodiversity (Horváth et al., 2012). These streams belong to the R-05 Broad category (Solheim et al., 2019). R-05 Broad category is defined as a small catchment area of less than 100 km², consisting of calcareous or mixed geology and an altitude below 200 m. (Fig. 1). The local climate exhibits an average annual temperature of 10.5°C, with an annual precipitation of cca. 550 mm and approximately 2050 h of sunshine each year (OMSZ, 2022). These small lowland streams are further characterized by a straight streambed, low slope, and gentle water current. Such conditions support a high abundance of macrophytes, and substantial levels of fine (FPOM) and coarse particulate organic matter (CPOM), which are derived from plant debris within the streambed (Borics et al., 2016). According to the Hungarian typology of running waters, based on the criteria introduced by the WFD, all studied streams belong to the same waterbody type, and they share the same regional species pool (Boda et al., 2023).

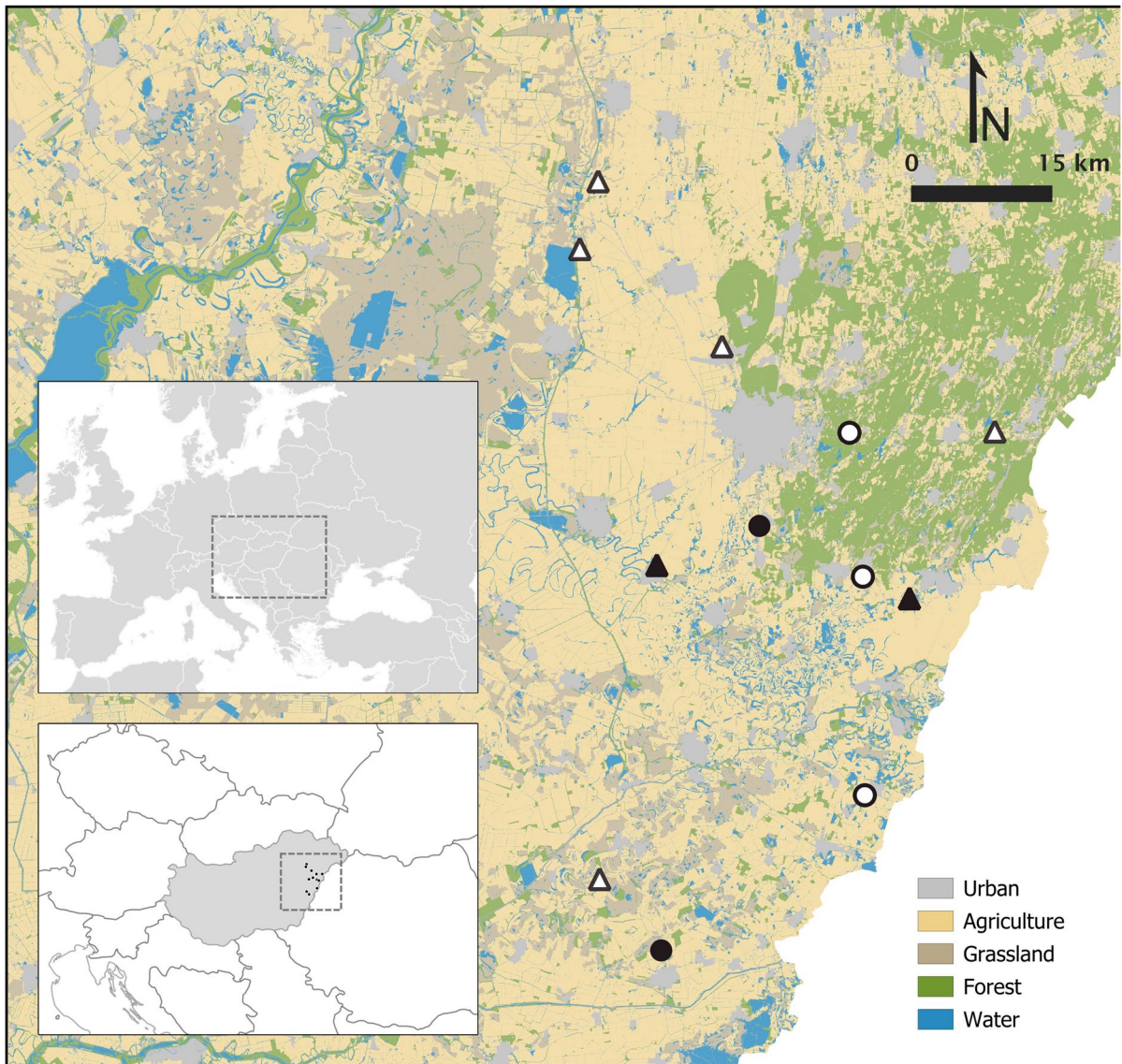


Fig. 1 Schematic map of the sampling area (Hungary, Europe). Site categories: ●—perennial good, ▲—perennial poor, ○—intermittent good, Δ—intermittent poor. Main land

use categories are represented as follows: grey for urban areas, yellow for agriculture, brown for grassland, green for forest, and blue for water bodies

In our study, we selected 12 streams (as shown in Fig. 1), which were categorized using two criteria: hydrological regimes and ecological potential. This dual categorization resulted in four distinct groups, which were later analyzed. The streams were divided into two hydrological categories. The first category, referred to as intermittent streams ($N=8$), includes streams that experience alternating flowing, non-flowing, and dry phases. While all of these streams

exhibit flow intermittency, the frequency and duration of dry periods vary among them. The second category, perennial streams ($N=4$), comprises streams that maintain continuous flow throughout the year without any cessation.

In addition to hydrological classification, the ecological potential of the streams was determined based on data from the National Monitoring System (RBMP 2, 2015). This classification followed the

methodology outlined in the Hungarian River Basin Management Plans for the 2013–2017 period (Government Decision 1155/2016. (III. 31.)). Ecological potential is a concept under the EU-WFD applied to heavily modified and artificial water bodies, reflecting the highest ecological condition achievable while accommodating the water body's designated use. In this study, the ecological potential was assessed using an intercalibrated quality assessment, which incorporates both abiotic (hydro-morphology, water chemistry) and biotic (macrophytes, phytoplankton, phyto-benthos, fish, aquatic macroinvertebrates) elements. The classification adheres to the EU Water Framework Directive's one-out, all-out principle, where the final status is determined by the lowest-performing quality element. For this study, we simplified the WFD categories and applied two broad ecological categories as follows. The "good" category includes streams with moderate and good quality status, while the "poor" category encompasses streams classified as having bad or poor ecological potential. As a result, seven streams were identified as having poor ecological potential, while five streams were classified as having good ecological potential.

Based on these dual categorizations, we have managed to create a total of four categories for our study (Table 1): *per_good*, *int_good*, *per_poor*, *int_poor*. Among these, the *per_good* category serves as a reference compared to the others, where at least one of the stressors (either flow intermittency or poor ecological potential) or both were present. (Online Resource 1).

Sampling method

Sampling was conducted on a monthly or bimonthly basis between 2020 and 2022, resulting in a total of 80 proposed sampling occasions. In case a streambed was not dry, sampling was carried out regardless of

the phases, flowing or non-flowing (pool) found. As a result of the sampling procedure outlined above, a total of 74 samples were taken from the 12 streams during the two years. The samples were collected based on the multi-habitat approach AQEM protocol developed for Hungary (Boda et al., 2023). The standardized kick-and-sweep technique was used with a standard pond-net with a 0.25×0.25 m frame and a 1-mm mesh. This method ensured that all habitat types were sampled proportionally along a 10 m section in all streams (Boda et al., 2023). One sample unit encompassed an area of 0.25×0.25 m, resulting in a total sampling area of 0.3125 square meters across 5 sample units, in the case of 10 sample units 0.625 m². We took five sample units in every site in every sampling occasion of the study area, the exception was two bad status streams because of an even site number in each category (Online Resource 1). To reduce the effect of differences in sampling effort we recalculated the number of genera by rarefaction using the iNext package (Hsieh et al., 2016). The abundance data were also standardized to 5 units in these sampling occasions. Samples were preserved in the field in 70% ethanol for laboratory sorting. Eleven major groups of invertebrates were studied, and all individuals were identified to species level (for Gastropoda, Bivalvia, Hirudinea, Crustacea, Ephemeroptera, Plecoptera, Odonata, Trichoptera, Heteroptera, Coleoptera), except for Diptera, which were identified to family level. The following references were used for identification (Lillehammer, 1988; Savage, 1989; Haybach, 1999; Csabai, 2000; Bauernfeind et al., 2001; Eggers & Martens, 2001; Andrikovics & Murányi, 2002; Csabai et al., 2002; Kontschán et al., 2002; Krno, 2004; Zwick, 2004; Eiseler, 2005; Waringer & Graf, 2011; Bauernfeind & Soldán, 2012; Dobson, 2012; Ambrus, 2018). Identified macroinvertebrates were preserved in 70% ethanol and stored in the laboratory.

Table 1 Dual categorization of streams with the name and abbreviations for categories, associated hydrological regimes and ecological potential, and the number of sampling occasions corresponding to each category

Categories	Categories abbreviation	Hydrological regime	Ecological potential	Number of sampling occasions
Perennial and good	<i>per_good</i>	Perennial	Good	20
Intermittent and good	<i>int_good</i>	Intermittent	Good	18
Perennial and poor	<i>per_poor</i>	Perennial	Poor	20
Intermittent and poor	<i>int_poor</i>	Intermittent	Poor	16

Data analyses

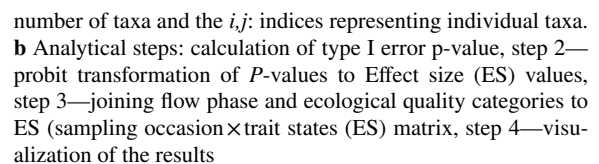
Although identification was mainly conducted at the species level, the absence of comprehensive species-level trait and functional databases, along with the possibility of incomplete data series, led us to use genus-level taxa lists. The DISPERSE database (Sarremejane et al., 2020) includes data for the majority of traits associated with European genera. Where the identification at the genus level was not possible (e.g. in the case of Diptera families), the mean of the trait state values for all genera within the corresponding taxonomic level was calculated and used as a single value. All available traits for macroinvertebrates from the DISPERSE database were used: maximum body size, life cycle duration, reproductive cycles per year, dispersal strategy, adult life span, female wing length, wing pair type, lifetime fecundity, propensity and also the main feeding type according to the Tachet's trait (Schmidt-Kloiber & Hering, 2015), (Online Resource 2). Consequently, our data analyses contained a matrix of 74 sampling events in four categories and 50 trait state data.

To examine the divergence and convergence of trait states, we utilized the null model-based workflow proposed by Lhotsky et al. (2016) and Borics et al. (2020). This workflow was modified to allow for comparisons between site groups (Várbíró et al., 2020).

The main steps of the analytical workflow are presented in Fig. 2. In the initial steps, we prepared the two data matrices: one matrix containing 74 sampling occasions and 135 genera, and the other for trait states with 138 genera and 50 traits. We employed Rao's quadratic entropy (RaoQ) (Botta-Dukát, 2005) on the generated 9,999 random samples by permutation with a randomization test restructuring trait state values among genera for each trait state as a null model which resulted in a $74 \times 50 \times 9,999$ random RaoQ distribution. The distance function was the simple matching coefficient (Botta-Dukát, 2005). In the first analytical step (Fig. 2, b. step 1) differences in trait state distributions between the real and random communities were characterized by the raw Type error *P*-values of the applied *t*-test. In the 2nd step, probit-transformed *P*-values were used as 'effect size values' (ES), which indicate a higher probability of trait divergence or convergence as raw *P*-values which often have a right-skewed distribution (Botta-Dukát,

2018). In the 3rd analytical step, we joined the hydrological regime flow phase and ecological potential category to the sampling occasion $\times$ trait state Effect Size matrix (74 sampling occasions $\times$ 50 trait states). The R code of the analyses can be found on the GitHub repository (https://github.com/varbirog/Macroinvertebrate_community_assembly_rules). The ranges of ES values of the categories show the driver forces (environmental filtering, limiting similarity). Positive ES values indicate that limiting similarity is the assembly rule, while negative values suggest that environmental filtering plays a primary role. When ES values are positive, it signifies that the species present in the assemblages have significantly different trait values compared to those in randomly assembled populations. Conversely, when ES values are negative, it indicates that the resident species have trait values that are more similar to each other than would be expected in randomized populations. This occurs because species with highly dissimilar trait values are screened out by environmental factors. This statistical approach, in combination with the randomization algorithm, enables the detection of both trait convergence resulting from environmental filtering and trait divergence due to limiting similarity (Botta-Dukát & Czúcz, 2016; Götzenberger et al., 2016). For determining the driver force of trait states we conducted *t*-tests on whether the ES values were different from zero in each category. The environmental filtering (trait convergence) and limiting similarity (trait divergence) were specified from the range of ES values by their median. Thus, we could test our first two hypotheses as the positive median of ES values indicates limiting similarity (LimSim) among genera of the existing community, while negative median values indicate environmental filtering (EnvFil). Then the driver force of each trait state was defined in separate categories, therefore the trait states could get two types of results: EnvFil, and LimSim. (Fig. 2, b. step 4). We compared the characteristics of each type considering all trait states and without rare trait states, defining trait states as rare if they possess less than 11 genera (lowest 20th percentile based on Online Resource 2).

To investigate hypothesis three the specific response of trait states to changes in driver force, we analyzed shifts in effect sizes (ES values) using the Mann–Whitney *U*-test. The "per_good" category serves as the initial reference state for assessing



Linear Discriminant Analysis (LDA) was conducted using the ‘MASS’ package to explore the discriminant power of the ES values on the different categories in the dataset (Fisher, 1936; Venables & Ripley, 2002). To visualize the differences between the four categories, we used the “ggstatplot” package (Patil, 2021). These boxplots were used for comparing the number of genera, number of individuals and ES values. Significant differences were calculated by the Kruskal–Wallis test. All statistical analyses were performed in R-software version 4.0.5. (R Development Core Team, 2021).

Results

A total of 135 genera were found during the sampling period. The highest rarefied taxon richness was in the *per_good* category (36 genera), and the lowest was in the *per_poor* category (1 genera). Significant differences ($P < 0.001$) were detected in taxon richness between the following categories: *per_good* vs. *per_poor* and *int_poor*, *int_good* vs. *per_poor* and *int_poor* (Fig. 3a).

A total of 110,959 individuals were collected during the sampling period. The highest rarefied number of individuals was in the *per_poor* category with a total of 9,232 individuals, while the lowest total of individuals was 42 in the *int_poor* category. A significant difference ($P < 0.01$) in abundance was detected between *int_poor* vs. *per_poor* and *int_good* categories (Fig. 3b).

The first axis of the LDA analysis (Fig. 4) performed on the ES values explained 55.38% of the variance, while the second axis explained 23.29%. The correct classification rate was 78.67% and the ES values distribution for trait states demonstrated a clear separation between categories. The *int_good*

category was distinct from the others, whereas the *per_poor* and *int_poor* showed overlaps.

In the case of 9 trait states, limiting similarity was exclusively the driver force in every categories, these are considered as neutral trait states (Table 2, Column of the Total number of categories in which the given trait states are driven by LimSim equal to number four). Despite the existence of categories where the driver force could not be determined, limiting similarity was the exclusive driver force for 2 trait states in 3 categories, for 3 trait states in 2 categories, and for 14 trait states in only 1 category (Table 2, Online Resource 3, Online Resource Figs. 1–10).

No trait states were found where environmental filtering was the exclusive driver force across all 4 or even in 3 categories. Despite the existence of categories where the driver force could not be determined, environmental filtering is exclusive for 6 trait states in 2 categories and for 8 trait states in only one category (Table 2, Column of Total number of categories in which the given trait states driven by EnvFil). Additionally, five trait states were influenced by both limiting similarity and environmental filtering as co-occurring driver forces across categories (Table 2, Online Resource 3, Online Resource Figs. 1–10).

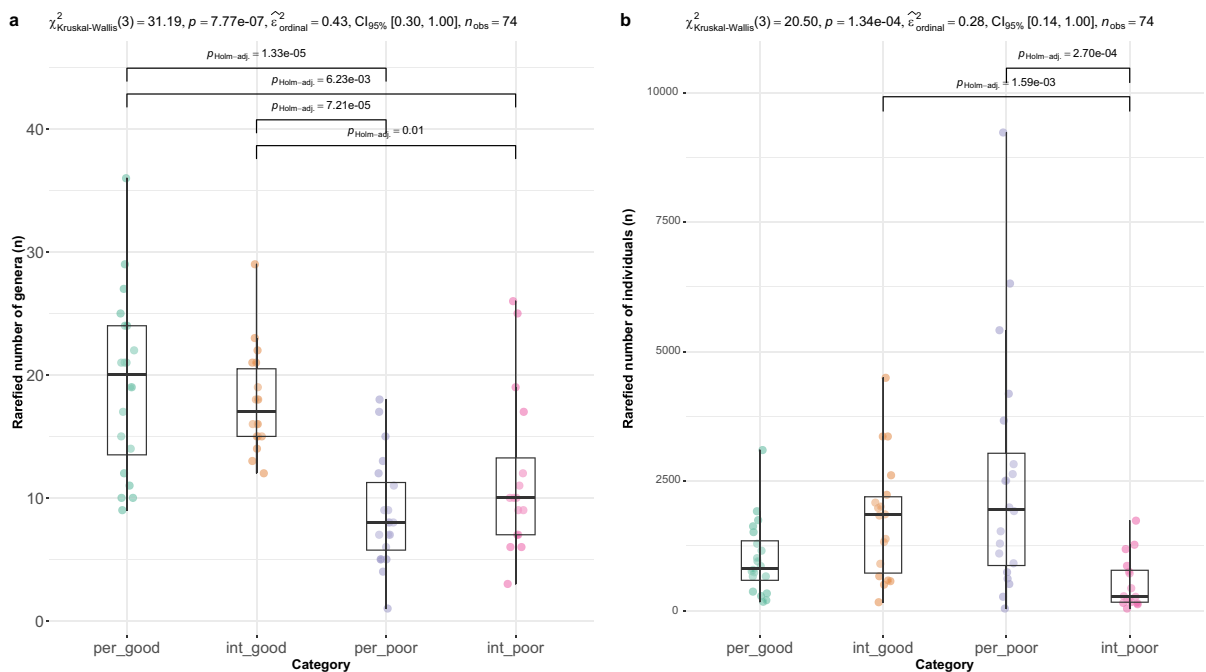


Fig. 3 Differences in **a** the rarefied number of genera, **b** the rarefied number of individuals across different categories

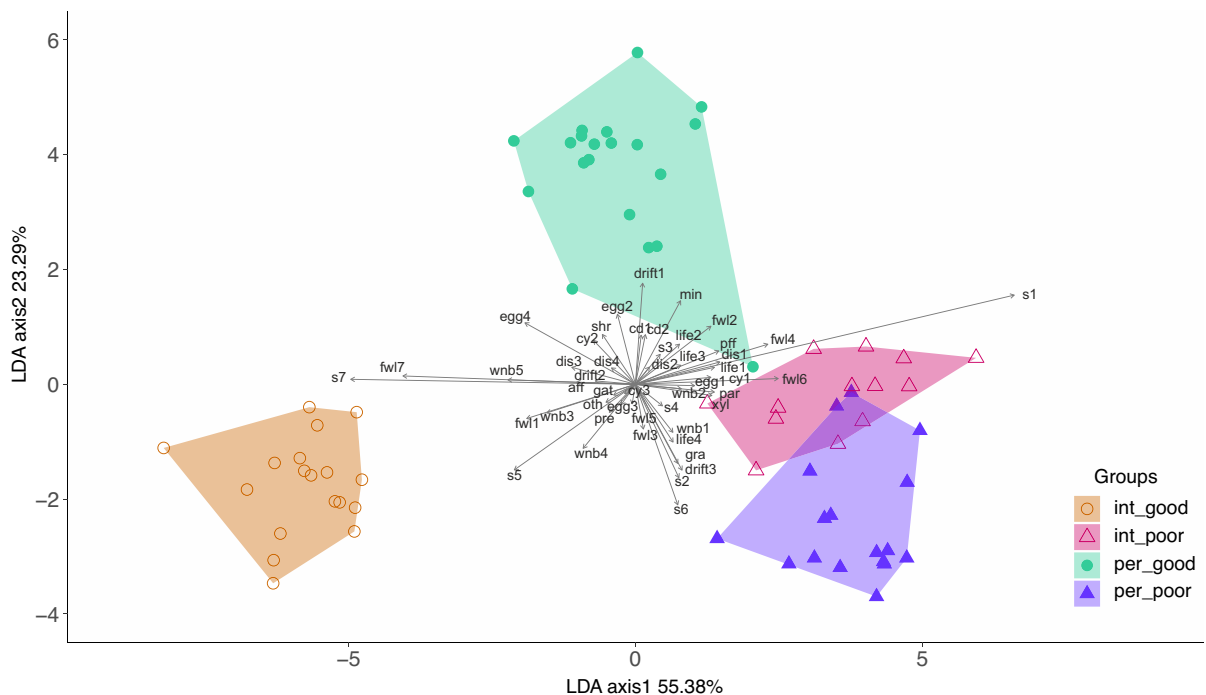


Fig. 4 Differences among categories based on linear discriminant analysis (LDA) using ES values of macroinvertebrate trait states

Regarding the categories, the *per_poor* category exhibited the highest incidence of the limiting similarity driver force, with 23 trait states, while the *int_good* category had the lowest occurrence of limiting similarity, with 12 trait states (Fig. 5a, Table 2 Row of Total number of trait states driven by LimSim). Conversely, the *int_good* category showed the highest occurrence of the environmental filtering driver force, with ten trait states, while the *per_poor* category had the lowest occurrence of environmental filtering, with only two TS (Fig. 5a, Table 2 Row of Total number of trait states driven by EnvFil). If we exclude rare trait states (less than 11 genera in the given trait), the importance of environmental filtering driver force further increases, which was more pronounced in the intermittent categories.

The Mann–Whitney *U*-test conducted on effect sizes (ES values) revealed specific responses of trait states to changes in driver forces (Online Resource 4). Significant shifts towards environmental filtering were observed in ten trait states: one in the *per_poor* category, four in the *int_good* category, and five in the *int_poor* category. In contrast, significant shifts towards limiting similarity were noted in twelve trait

states: two in the *per_poor* category, eight in the *int_good* category, and two in the *int_poor* category (Fig. 6a, b, Online Resource 4). Three trait states show significant cross-shift changes in response to the single (flow intermittency) stressor. *Predators* (Fig. 6b: pre) exhibit environmental filtering in perennial streams with good ecological potential but limiting similarity in *int_good* streams. For trait states of *short life span* (Fig. 6c: life2, Online Resource 4) and *aquatic active* (Fig. 6c: dis2, Online Resource 4), there is an opposite trend in the shift. No cross-shift was observed as a response to either the single (poor ecological potential) or the combined stressor (poor ecological potential and flow intermittency).

Discussion

Using the community assembly framework, we investigated the impact of the concurrent or individual presence of two stresses on the structural and functional attributes of the aquatic macroinvertebrate community. We identified neutral trait states that remained consistent and did not vary

Table 2 Summary table of the driver forces (deviations from random distribution) affecting trait states across all traits

Trait name	Trait state description	Trait state code	Taxon number	per_good	int_good	per_poor	int_poor	Total number of categories in which the given trait states driven by	
								EnvFil	LimSim
Life cycle duration	≤ 1 year	cd1	106						
	> 1 year	cd2	87						
Potential number of reproductive cycles per year	< 1	cy1	25	↓			↓	2	
	1	cy2	120	↑		↑			2
	> 1	cy3	79			↑			1
Dispersal strategy	Aquatic passive	dis1	85		↓	↑		1	1
	Aquatic active	dis2	121	↑	↓	↑		1	2
	Aerial passive	dis3	34	↑		↑	↑		3
	Aerial active	dis4	90						
Propensity to drift	Rare/catastrophic	drift1	114				↑		1
	Occasional	drift2	29			↑			1
	Frequent	drift3	14	↑	↑	↑	↑		4
Lifelong fecundity (number of eggs per female)	< 100	egg1	82			↓		1	
	≥ 100 to 1000	egg2	80						
	≥ 1000 to 3000	egg3	27						
	≥ 3000	egg4	11	↑	↑	↑	↑		4
Feeding type	Active filter feeders	aff	11			↑			1
	Gatherers-collectors	gat	39		↓	↑	↓	2	1
	Grazers-scrappers	gra	40			↑			1
	Miners	min	4*	↑	↑	↑	↑		4
	Other	oth	17		↑		↑		2
	Parasites	par	5*	↑	↑	↑	↑		4
	Passive filter feeders	pff	4*	↑	↑	↑	↑		4
	Predators	pre	72	↓	↑			1	1
	Shredders	shr	34				↓	1	
	Xylophagous	xyl	1*	↑	↑	↑	↑		4
	< 5	fwl1	42	↑					1
	≥ 5 to 10	fwl2	41		↓	↓		2	
	≥ 10 to 15	fwl3	29		↓		↓	2	
Female wing length (mm)	≥ 15 to 20	fwl4	18		↓			1	
	≥ 20 to 30	fwl5	13	↓	↓			2	
	≥ 30 to 40	fwl6	7*			↑			1
	≥ 40 to 50	fwl7	2*	↑	↑	↑	↑		4
	≥ 50	fwl8	0						

Table 2 (continued)

Trait name	Trait state description	Trait state code	Taxon number	per_good	int_good	per_poor	int_poor	Total number of categories in which the given trait states driven by	
								EnvFil	LimSim
Adult life span	< 1 week	life1	17			↑		1	
	≥ 1 week to 1 month	life2	24	↑	↓			1	1
	≥ 1 month to 1 year	life3	94						
	≥ 1 year	life4	66						
Maximum body size (cm)	< 0.25	s1	3*	↑	↑	↑	↑		4
	≥ 0.25 to 0.5	s2	40						
	≥ 0.5 to 1	s3	63						
	≥ 1 to 2	s4	69			↑			1
	≥ 2 to 4	s5	47						
	≥ 4 to 8	s6	15	↓	↓			2	
	≥ 8	s7	2*	↑	↑	↑	↑		4
Wing pair type	No wings	wnb1	36			↑			1
	1 pair+ halteres	wnb2	14						
	1 pair+ 1 pair of small hind wings	wnb3	5*		↑	↑	↑		3
	1 pair+ 1 pair of elytra or hemielytra	wnb4	49						
	2 similar-sized pairs	wnb5	24		↓			1	
Total number of trait states driven by		EnvFil		4	10	2	4		
		LimSim		14	12	23	13		

The table presents the trait name, trait state description, trait state code, the number of taxa possessing each trait state, and the driver forces for each category, along with their totals by category and trait states. Only the significant differences are shown, and the rare states are marked with an asterisk (*), ↓: Environmental filtering—EnvFil; ↑: Limiting similarity – LimSim

across different environmental conditions, indicating limiting similarity across all environmental categories. We confirmed that both in unstressed and in single-stressed environments (poor ecological conditions), limiting similarity is the primary driver force that shapes the structure of the macroinvertebrate community. We highlighted that it is not the quantity but rather the quality (or type) of stress that increases the influence of environmental filtering. Furthermore, specific trait states were detected under different types of stress. All of these findings allow for a more nuanced approach to conservation,

considering the specific roles of taxa possessing combined trait states in ecological processes.

Comparison of functional changes among categories

Since stressors are selected through trait states, but traits are possessed by species, it is worthwhile to analyze community structural changes from a functional perspective (Chalmandrier et al., 2021; Mitwally, 2022). In a functional context, the *per_good* category was more similar to the *int_poor* than *per_poor* category. Thus, with multi- stressors, the

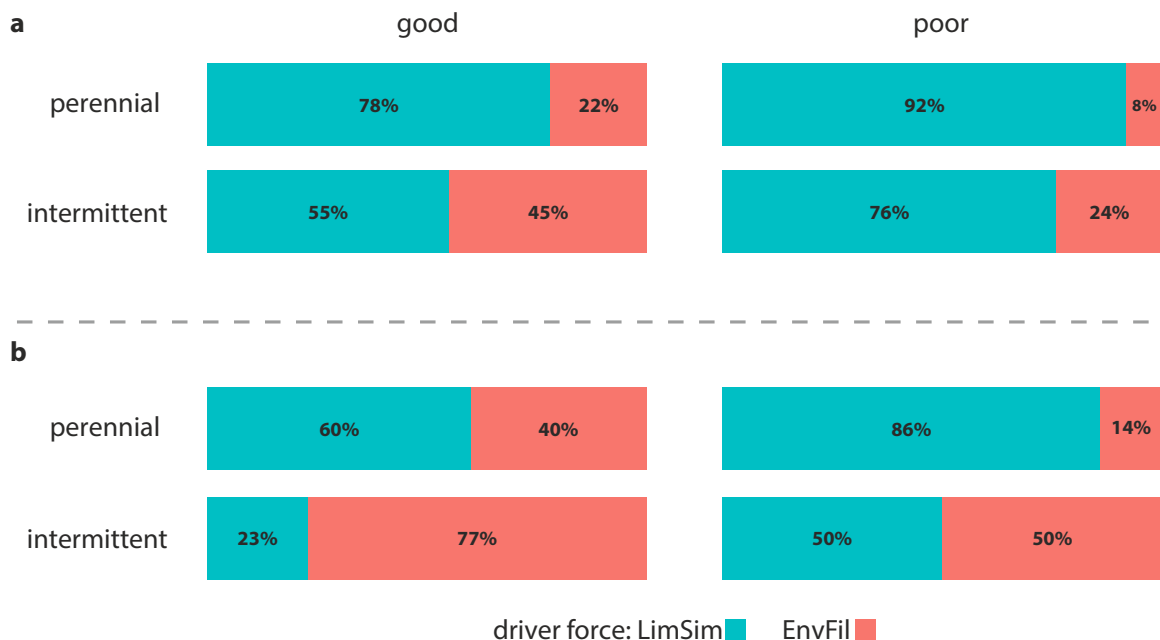


Fig. 5 Primary driver forces in categories. Percentage of trait states which belong to driver forces (EnvFil, LimSim) in different hydrological regimes and different ecological potential, **a** all trait states, **b** without rare trait states

functional differences were less pronounced, whereas with a single stressors, the differences between the categories were more distinct. This suggests that the simultaneous presence of stressors has an antagonistic rather than synergistic effect on the macroinvertebrate communities. This result has also been confirmed in artificial environments, where the combined effects of drying and nutrient enrichment were found to be antagonistic, with drying mitigating the more severe impacts of nutrient enrichment (Loskotová et al., 2023). Further research is needed to understand the precise mechanisms of interactions between stressors in various climatic and geographic contexts to better elucidate their effects on aquatic communities because antagonistic or synergistic effects depend on the environmental conditions (Kefford et al., 2023). In perennial streams, regardless of their ecological potential, processes such as dispersal and species interactions have already taken place, resulting in a stable community structure and abundance (Simmons et al., 2021). However, it is important to acknowledge that as various disturbances, such as extreme hydrological events, anthropogenic impacts, or invasive species, may also disrupt stability in perennial streams (Lake, 2000; Lawrence et al., 2010). Contrary

to this, intermittent conditions can enhance ecological processes during the rewetting phase, ultimately shaping assemblages both structurally and functionally. After dry phases, dispersal intensifies, competition escalates, and environmental filtering strengthens in newly created habitats. This is supported by previous studies on primary succession and newly created habitats (Vander Vorste et al., 2016; Crabot et al., 2020; Fournier et al., 2023). The influx of species into empty niches during the rewetting phase resembles the colonization of newly created habitats, where ecological processes play a crucial role in building the assemblage (Doretto et al., 2020). Therefore, the analogy between the rewetting phase and newly created habitats suggests that intermittent conditions can enhance the processes that shape assemblages after flow cessation (Crabot et al., 2021). Additionally, even the drying phases themselves might allow certain perennial stream taxa to temporarily persist or re-establish after disturbances, as highlighted in studies focusing on resilience dynamics in lotic ecosystems (Bozóki et al., 2024). Drying creates an opportunity for new taxa to become community members (Nimmo et al., 2015) if they can successfully survive the ecological processes (Lytle & Poff, 2004).

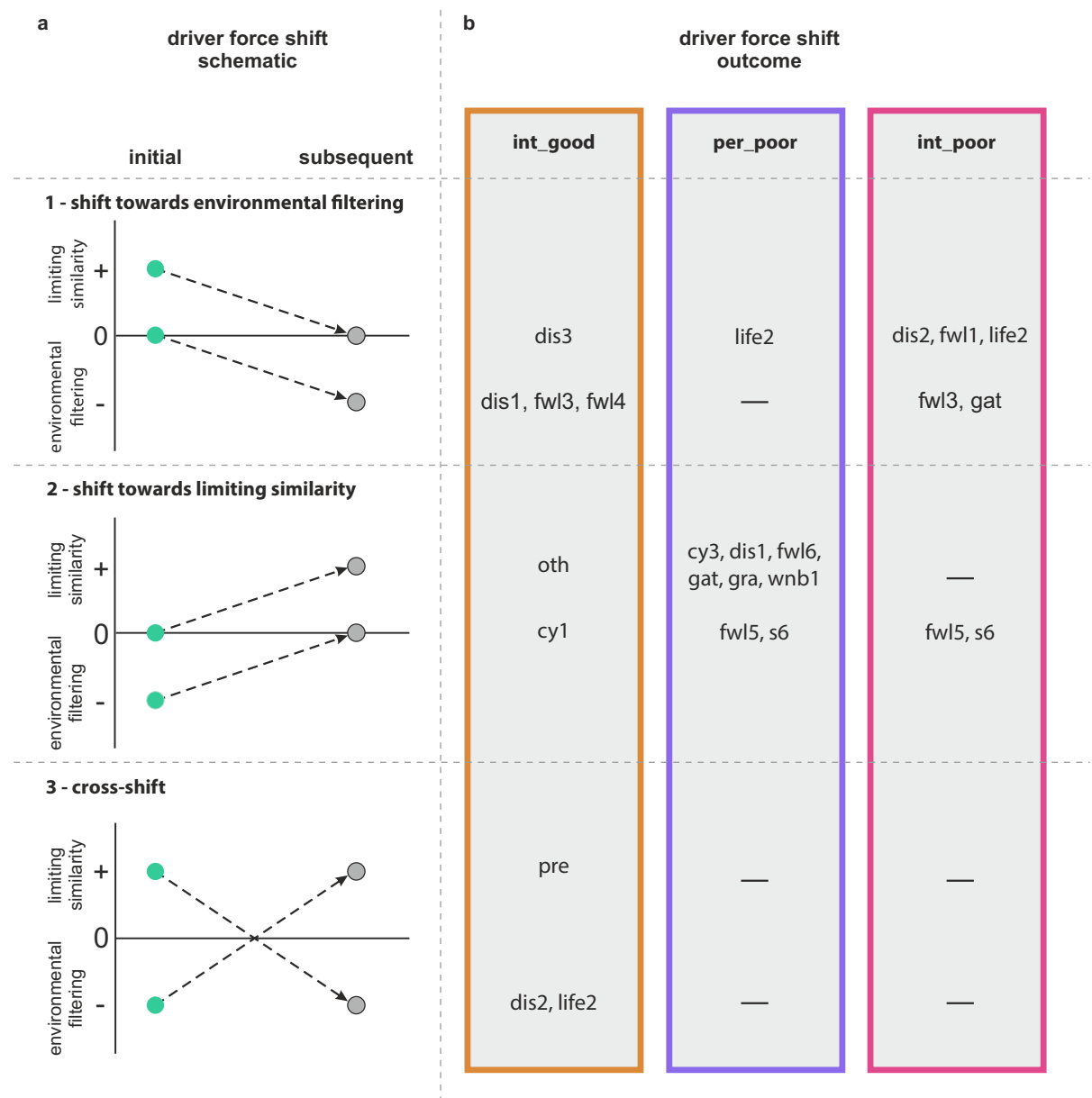


Fig. 6 The specific trait states responses, significant driver force shifts of trait states compared to the perennial good (*per_good*) category, **a** driver force shift schematic graphic 1 shift towards environmental filtering 2 shift towards limiting

similarity, 3 cross-shift. **b** driver force shift outcome, indicating trait state abbreviation in each driver force shift category. The name of the trait states' abbreviations are shown in Online Resource 2

The dynamics of ecological processes were not difference in the case of the same ecological potential and resulted in lower species richness in the case of poor categories. Abundance ratios also significantly influence community structure. The *per_poor* and *int_good* categories have a higher abundance

than the *int_good* category. While there was a significant difference in species numbers, the *per_good* and *int_poor* do not differ for abundance. The flow intermittency in different ecological potentials leads to different abundance ratios. These differences in the dynamics of ecological processes result in the

functional composition (based on ES values) of the *int_poor* category being more similar to *per_good* than to all others.

Neutral trait states

Trait states show various responses to single (Bozóki et al., 2024) or multi-stressors (Calapez et al., 2018) as expected based on previous studies. For most trait states, it cannot be determined unequivocally whether limiting similarity or environmental filtering is the governing principle regarding their probability of presence, as in these trait states species occur randomly. However, the predictions were successfully supported by our results for some trait states.

Several trait states are neutral and do not exhibit specific driver forces under different environmental pressures. From all categories limiting similarity was exclusively the driver force in the case of 9 trait states. Among these trait states there are biological traits such as the $\geq 3,000$ number of eggs per female (egg4) of lifelong fecundity, ecological traits such as the *miners*, *passive filter feeders*, *xylophagous* and *parasites* of feeding type, and also behavioral traits such as *frequent* (drift3) of propensity to drift or morphological traits as ≥ 40 to 50 mm (fwl7) of female wing length, and < 0.25 cm (s1) and > 8 cm (s7) of maximum body size. In the case of rare trait states like the *xylophagous* and *parasites* trait states the results are derived from a limited dataset and must be therefore considered as artifacts in the absence of ecological relevance. For others, ecological stability and resilience within the community were presumed, defined as the capacity of trait states to maintain functionality and recover from disturbances (Bogan et al., 2015). Small body size and high fecundity can facilitate rapid population recovery after disturbances (Mykrä et al., 2007), while high dispersal ability allows macroinvertebrates to colonize habitats efficiently (Řezníčková et al. 2007; Pařil et al., 2019). The combination of these trait states by promoting rapid recovery, efficient resource utilization, and adaptability to changing environmental conditions enables macroinvertebrates to respond effectively to poor ecological conditions and flow intermittency. This adaptability allows them to persist and thrive in dynamic ecosystems undergoing poor ecological conditions or flow intermittency (Booth et al., 2016). The presence of neutral trait states indicates that they are

consistently beneficial for the organisms in the community, regardless of external pressures. These trait states might lead to functional redundancy, where multiple species share similar ecological functions (Belmar et al., 2019). This redundancy can increase the ability of the community to withstand disturbances (e.g. flow intermittency and poor ecological condition), as there are multiple species capable of performing similar functions (Schmera et al., 2017; Wang et al., 2023).

Effect of flow intermittency vs. ecological potential

The higher number of trait states belonging to limiting similarity across all categories suggests that coexisting species in the community tend to have more distinct ecological traits. This indicates a consistent pattern, where species within the community exhibit a greater divergence in their trait states, regardless of specific environmental conditions, such as flow intermittency or poor ecological condition. This could imply that the ecological processes are leading to a more pronounced limiting similarity effect. However, the percentage of limiting similarity and environmental filtering varied among trait states of categories.

In intermittent water regimes, environmental filtering is higher in good ecological conditions than in poor ones suggesting that the structuring of the community is more influenced by specific environmental factors in streams with good ecological potential. Additionally, it has been observed that intermittent streams with longer flowing periods have more diverse macroinvertebrate communities, likely due to increased habitat heterogeneity and resource availability during the wet phase (Calabrese et al., 2020).

In a less degraded environment—regardless of flow intermittency—conditions are generally suitable for several species, and certain trait states become more critical for species to persist (Menegotto et al., 2019). This might lead to a stronger environmental filtering effect, where species with particular trait states that align with the prevailing environmental conditions are more likely to be a member of the community. Less favorable, poor environmental conditions, however, might have a more equalizing effect on the community. Species with a broader range of trait states might persist due to the challenging ecological conditions, and the filtering effect might be less pronounced compared to the more selective

influence of environmental factors in good conditions. Overall, higher environmental filtering in good environmental conditions signifies a more selective process driven by specific environmental factors, contributing to a more distinct community structure based on trait selection (Murray-Stoker et al., 2022).

In perennial flow regimes, limiting similarity is equally dominant in both good and poor environmental conditions which suggests that the influence of limiting similarity on community structure remains consistent regardless of the overall environmental quality. The limiting similarity effect, which refers to the tendency of coexisting species to differ in their ecological trait states, does not vary significantly based on the overall environmental conditions. This may indicate that species in the community tend to differentiate their trait states from each other to a similar extent, irrespective of the presence of other stressors (e.g. poor ecological conditions) (Calabrese et al., 2020). It could imply that certain ecological processes related to trait-based interactions are robust and operate consistently, while community structures are relatively stable and are not strongly modulated by the overall environmental quality. Regardless of the ecological conditions, in streams with perennial water regimes, species with more diverse trait states can coexist. Perennial environmental conditions, favor certain trait combinations or ecological strategies, leading to a community with a higher trait state diversity. On the contrary, in streams with intermittent water regimes, the limiting similarity is lower, indicating lower trait state diversity.

The higher influence of environmental filtering in intermittent streams with good ecological potential suggests that flow intermittency has a more pronounced effect on the aquatic community than poor ecological conditions. When considering only rare trait states rather than all trait states, this phenomenon is more pronounced indicating that general trait patterns are more sensitive to flow intermittency (Wooster & DeBano, 2018). A clear explanation might be that abrupt drying events entirely eliminate the living conditions, while poor ecological conditions merely restrict them.

Specific trait state responses

We observed specific trait states (shift towards limiting similarity) specifically concerning the number of

reproductive cycles per year (cyl), in connection to intermittency. This phenomenon reflects findings in Mediterranean salt marsh ponds, where the interplay of water permanence and hydrological variability similarly influences macroinvertebrate communities (Gascón et al., 2007). Certain trait states, for example, gatherers-collectors, show opposite patterns (shift towards environmental filtering) concerning intermittent poor ecological conditions. This reflects the results of studies suggesting that water quality, habitat structure, and human activities affect the abundance and distribution of aquatic macroinvertebrates, including collector-gatherers, collector-filterers, and collector-scrappers, which in turn influence stream-ecosystem processes and indicate water quality changes (Wallace & Webster, 1996; Hieber Ruiz et al., 2005; Addo-Bediako, 2021). These findings highlight the importance of considering specific traits and their trait states' relationship to environmental conditions when studying community assembly and environmental filtering.

Only three trait states show specific responses and demonstrate different driver forces across various environmental conditions. Different mechanisms govern the probability of species possessing these trait states in response to environmental conditions. *Predators* being under environmental filtering in perennial streams with good ecological potential but under limiting similarity in intermittent streams suggests that different ecological processes influence predator communities under stable and unstable hydrological conditions. Limiting similarity indicates that predators in intermittent streams can occupy specific niches. The shift to limiting similarity in intermittent streams indicates that the predator community is not influenced by intermittency and plays a more dominant role in shaping their assemblages. In intermittent environments, the diversity of predator species is lower, while their abundance tends to be higher (Schriever & Lytle, 2016). This phenomenon known as a “predator soup” can occur when pools are formed in intermittent streams, highlighting the impact of intermittency on predator assemblages (Bogan & Lytle, 2007; Boulton & Lake, 2008).

On the contrary, we found that for taxa with *short life spans* and *aquatic active* state of dispersal strategy, there is an opposite trend. In intermittent habitats, environmental filtering has a significant influence on these trait states, resulting in the lower probability

of the occurrence of these taxa than what would be expected. Although, in a recent study, an increasing trend was observed in intermittent streams richness of warm-adapted taxa with aquatic active trait states (Gebert et al., 2022), however, *aquatic active* trait state is associated with recovered with recovery community of the streams from after dry events. Our results imply that in perennial water bodies, the presence probability of taxa with *short life spans* and *aquatic active* trait states is stable, but unstable in intermittent streams. Thus, in variable hydrological environments, environmental filtering is the driver force of *aquatic active* and *short life span* trait states. This could be because, during flow intermittency, these trait states lose their relative competitive advantage in favor of other trait states.

Conclusion

The frequency of floods and flow intermittency in Europe is expected to increase due to climate change (Döll & Schmied, 2012). This will have significant consequences for freshwater habitats and require the implementation of effective management strategies (Edwards, 2012). Aquatic insects cannot optimize their performance in all niche dimensions simultaneously, indicating the need for more data and long-term studies (Bonada et al., 2006). Additionally, we confirmed our prediction by identifying neutral trait states that remain unchanged under different stressors. Our findings confirmed that unstressed environments, limiting similarity predominantly shape community structure, supporting our hypothesis. We also found that the effect of environmental filtering is more dependent on the type of stress than its intensity. We also found specific trait states that respond uniquely to various stresses. By understanding these roles and contributions, conservationists can develop targeted strategies that maintain or restore key ecological processes, ensure the resilience and stability of ecosystems, and prioritize actions that support biodiversity and ecosystem services essential for human well-being.

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Data availability The data that support the findings of this study are available from https://github.com/varbirog/Macro_invertebrate_community_assembly_rules.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

Ethical approval Not applicable.

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