

Evolutionary responses of aquatic macroinvertebrates to two contrasting flow regimes

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Abstract Natural disturbances are agents of natural selection that drive multiple biological adaptations along evolutionary time. Frequent, high magnitude disturbances are expected to select for morphological and behavioral traits to resist or to avoid them. In contrast, predictable and seasonal disturbances are expected to select for synchronized life cycles to avoid unfavorable periods. We assessed the effect of flood disturbances on aquatic macroinvertebrates in two rivers with contrasting flow regimes: the Gila (USA)

with seasonal floods and droughts, and the Thur (Switzerland) with a high frequency of aseasonal floods. Macroinvertebrates were analyzed based on 46 biological trait categories classified into morphological, life-cycle synchronization, and behavioral strategies. Flood effects on diversity and composition were much clearer for the Gila than for the Thur. Overall, biological adaptations were related to the flood regime of each river. Morphological adaptations to resist or avoid floods prevailed under frequent and aseasonal disturbances (the Thur), whereas life-cycle synchronization and behavioral adaptations were associated with highly seasonal, predictable, and low-frequency disturbances (the Gila). Given that forecasted future flow regimes differ between regions, our results suggest that the effects of future flow regime

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alterations will ultimately depend on the adaptation strategies to current flow regimes.

Keywords Droughts · Floods · Predictability · Resilience · Resistance · River ecosystems

Introduction

Natural disturbances are key factors that influence population and community dynamics, as well as ecosystem structure and functioning (Lake, 2000). They are thus agents of natural selection and drive biological adaptations along evolutionary time (Lytle, 2001). The disturbance regime, characterized by frequency, predictability, timing, and magnitude, influences the extent to which such adaptations may evolve (Lytle et al., 2008). Rare and high magnitude disturbances, such as earthquakes, volcanic eruptions, or tornados, have low evolutionary power in contrast to frequent and predictable events that trigger rapid evolutionary adaptations (Lytle, 2001) because they are sporadic. Understanding how adaptations have evolved and, consequently, how the functional community profile has changed in response to natural disturbance regimes is fundamental to elucidate the mechanisms of natural selection and species sorting operating in ecosystems.

In river ecosystems, floods and droughts are considered as major natural disturbances. Floods are pulse disturbances that occur in a relatively short period of time, whereas droughts act as ramp disturbances that occur gradually and may persist for long periods (Lake, 2000). Both types of disturbances modify habitat availability, disrupt ecosystem processes, and impose different constraints on aquatic life (e.g., Calapez et al., 2014; Bae & Park, 2017; Piniewski et al., 2017). The environmental effects of floods have long been recognized compared to those of droughts, probably because floods are more universal than droughts (Lake, 2011). Floods are components of

the hydrological variability of all river ecosystems, whereas droughts are only characteristic of particular river types in different climatic regions. Extreme flow events mobilize the substrate, increase suspended organic matter and inorganic sediments, and wash out flora and fauna, whereas extreme droughts cause mortality via the elimination of aquatic habitat (Poff & Ward, 1989; Robinson et al., 2004). Both disturbance events ultimately reduce diversity and abundance of macroinvertebrates (Robinson et al., 2004; Death, 2008).

Aquatic organisms have evolved morphological, life history, and behavioral adaptations to resist or to avoid floods and droughts (Lytle & Poff, 2004). Resistance (or endurance) strategies include those that allow organisms to withstand flow disturbance by acquired features as an adaptation response, such as the presence of suckers in stream macroinvertebrates that enable resistance to floods or the resistance cysts of stream macroinvertebrates that enable resistance to droughts (Bonada et al., 2007; Hershkovitz & Gasith, 2013). Alternatively, stream organisms have also evolved avoidance strategies to escape from flow disturbances by moving temporarily to a refuge (e.g., to terrestrial habitats during floods or to distant aquatic habitats by long-distance aerial dispersal during droughts; Bonada et al., 2007; Lytle et al., 2008; Hershkovitz & Gasith, 2013). However, despite resistance/avoidance strategies being recognized in almost all groups of aquatic organisms (Lytle & Poff, 2004), resilience strategies are also very common. Resilience strategies, such as short life cycles or rapid growth rates, allow for a rapid recovery from flow disturbances (Hershkovitz & Gasith, 2013) and the restoration of diversity and abundance to levels similar to that before a disturbance event (Robinson et al., 2003, 2004).

Acquired evolutionary responses to survive floods and droughts mainly depend on the frequency, magnitude, predictability, and timing of flow disturbances. Lytle & Poff (2004) suggested that frequency and magnitude are important attributes for selecting resistance strategies, whereas predictability and timing are important for avoidance strategies. Thus, frequent and/or severe floods and droughts may favor aquatic organisms with morphological adaptations that enable them to withstand flow changes and rapidly recolonize. In contrast, infrequent and mild floods would exert a low selection pressure on aquatic organisms,

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and species composition would be driven by stochastic events of colonization and extinction instead of environmental filtering (Robinson et al., 2003). Highly predictable and seasonal floods and droughts would favor aquatic organisms with synchronized life cycles, whereas low predictability and aseasonal floods and droughts would select for organisms with rapid responses to flow disturbances by particular behavioral characteristics (e.g., ability to move temporarily to a refuge).

Flood and drought attributes are not uniform worldwide. Different climates result in different flow regimes, and thus different attributes of floods and droughts (Poff & Ward, 1989; Lepori & Hjerdt, 2006). For example, a mediterranean-type climate exhibits highly predictable floods with a particular timing (i.e., spring and autumn especially), while in temperate climate regions floods have relatively low predictability and are therefore aseasonal (Bonada & Resh, 2013). As attributes of floods and droughts differ among climates, different climate regions should have different adaptive traits to floods and droughts in the sense described by Lytle & Poff (2004).

Flow regimes are changing worldwide as a result of human activities (Poff et al., 1997). River flow has been regulated by dams and reduced by withdrawals for domestic, agricultural, or industrial uses, modifying hydrology, connectivity, and the related catchment processes (e.g., McCluney et al., 2014; Schneider & Petrin, 2017). Furthermore, different hydrological models predict that flow regimes will be modified in the near future as a result of global climate change. The frequency, magnitude, predictability, and timing of floods and droughts will be affected differently in each climatic region of the world (e.g., Schneider et al., 2012). For example, flow magnitude is predicted to change in the Mediterranean and central Europe, whereas flow timing is likely to be more affected in boreal areas (Schneider et al., 2012). Aquatic organisms will be affected directly or indirectly by climate change (via flow regime alterations), at a rate even higher than terrestrial organisms (Vörösmarty et al., 2010), with potential impacts on ecosystem functioning (Woodward et al., 2016). The vulnerability of aquatic organisms to flow regime alteration, however, will ultimately depend on their adaptations to the natural flow regime of each climatic region (Lytle & Poff, 2004). For example, organisms having costly resistance strategies to withstand floods will be

vulnerable if floods diminish due to climate change, because other strategies that require fewer constraints could be favored. However, these resistance strategies will become advantageous if flood frequency increases or become unpredictable.

In this study, we compared flood resistance and avoidance strategies of macroinvertebrate communities in two river basins with contrasting natural flow regimes: one in a semi-arid and another in a temperate region. Streams in the semi-arid region are characterized by low to no-flow conditions during the dry period and a distinct flood period during summer (monsoonal rains). Moreover, there is substantial interannual variation in the magnitude of the flow, driven by the occurrence of El Niño and La Niña years (Molles & Dahm, 1990). In contrast, flow patterns of streams in the temperate region are characterized by frequent floods almost randomly distributed in time and the lack of no-flow periods (Uehlinger, 2000).

We assessed the effects of the flood period on the macroinvertebrate community structure (i.e., genus composition) and function (i.e., biological trait composition) with the aim of identifying the biological adaptations to floods in each region. Because floods are known to reduce the abundance and diversity of macroinvertebrate communities by washing out individuals (Robinson et al., 2004), we expected a similar response to floods in both climate regions with respect to abundance, and structural and functional diversity. However, because both climate regions differ in the frequency, predictability, timing, and magnitude of floods, the biological adaptations to withstand, avoid, and recover from floods are expected to differ. Based on the framework of Lytle & Poff (2004), we expected that morphological and behavioral adaptations to resist or avoid floods would prevail in temperate regions because floods are more frequent, aseasonal, and therefore unpredictable. In contrast, life-cycle synchronization adaptations to avoid floods were expected to be more important in the semi-arid region as a result of highly predictable floods and droughts. Our results can thus provide insights to understand how natural communities have evolved adaptations in response to disturbance regimes, and information about the mechanisms through which communities will be affected by flow regime alterations.

Methods

Site description

Two river basins with contrasting natural flow regimes were selected: the Gila in a semi-arid region and the Thur in a temperate region. Cross-basin studies that include before and after disturbance event sampling are rare. Most studies analyzing the effects of floods or extreme flow events over time have focused only on a single basin or on a single significant flood or drought event (e.g., Robinson et al., 2003; Feeley et al., 2012; Woodward et al., 2015) and many studies lack before flood data (Piniewski et al., 2017). In our study, to avoid the lack of basin replication, several sites were chosen along each basin and stream order was used as a covariable in the statistical analyses. This approach was also adopted to reduce variability among sites within each basin (located at different stream orders) and to increase statistical power.

The Gila River, located in the southwestern USA, is a tributary of the Colorado River (Supplementary Material S1). It is located in an arid and semi-arid climate region with subtropical influences. Precipitation is mostly associated with the Mexican or North American monsoon, with 70% of the annual precipitation falling between July and September (Acuña & Dahm, 2007). These intense summer rains contrast with the extremely dry conditions of the rest of the year. The headwaters of the Gila drain the Mogollon Mountains (8981 km²) and are among the few free-flowing rivers left in North America (Acuña & Dahm, 2007).

Elevation in the Datil-Mogollon section ranges from 3320 m a.s.l. at Whitewater Baldy in the Mogollon Mountains to 1463 m a.s.l. at the Gila River Valley. The major land cover categories in the Gila Basin are extensive forest areas at higher elevations and rangeland in most of the rest of the catchment. Small urban and agricultural communities are only present along the lower river valley in the Gila Cliff area.

Nine study sites were selected from within the upper part the Gila Basin, aiming to encompass differences in thermal and flow conditions, as well as in geomorphology (Table 1). All sites were located at altitudes higher than 1300 m a.s.l. but differed in stream order, drainage area, and slope. Stream order varied from 3 to 7 and drainage area ranged from 43 to

8981 km² (Table 1). Sediment size at the study sites varied from 0.005 to 0.120 m (D₅₀, Table 1). Overall, total suspended solids increased with stream order, and oxygen values were similar in all study sites (TSS and DO, Table 1). Only one site had a high average value of TSS but with a high standard deviation.

The Thur River, located in northeastern Switzerland, is a tributary of the upper Rhine (Supplementary Material S1) and is located in a temperate climate region. Winter conditions are cold at the upper sites and relatively mild at the lower sites due to an oceanic influence. Precipitation is relatively high (1200–1800 mm) with a minimum in February and a maximum in June/July. The headwaters of the Thur drain an Alpine region (maximum altitude: 2502 m a.s.l.), but about 60% of the basin is in the foothills of the Alps (600–1800 m a.s.l.) and in the Swiss plateau (370–600 m a.s.l.). Land cover in the Thur Basin is primarily composed of fields, orchards and pasture (61%), forest (25%), and urban areas (8%) (Uehlinger, 2000).

Seven study sites were selected from within the entire network of the Thur Basin, aiming to encompass differences in thermal and flow conditions, as well as in geomorphology (Table 1). In contrast to the Gila, sites were located at lower altitudes but also differed in stream order, drainage area, and slope. Stream order varied from 4 to 7 and drainage area ranged from 17 to 1648 km² (Table 1). The substrate of the river bottom was mainly composed of pebbles and gravels although bedrock outcrops also occurred at a few sites (D₅₀ ranged from 0.051 to 0.155 m; Table 1). As in the Gila, total suspended solids overall increased with stream order, and oxygen values were similar in all study sites (TSS and DO, Table 1).

Flow regime characteristics

Discharge data from the Gila Basin were obtained from three United States Geological Survey (USGS) gaging stations, one at Mogollon Creek downstream of the confluence with Rain Creek (USGS 09430600) (sites G7, G8, and G9), and two in the Gila River (G2—USGS 09430500; and G1—USGS 09431500). Discharge data from the Thur Basin were obtained from 4 gaging stations of the Federal Office for the Environment (Switzerland) located at sites T1, T2, T5, and T6. There are no large dams in the Thur Basin or in the sampled Gila Basin affecting natural flow regimes

Table 1 Study site characteristics

Basin	Code	Site	Altitude (m a.s.l.)	Stream order (geomorphic definition)	Drainage area (km ²)	Slope (m/m)	Sediment size D ₅₀ (m)	Average TSS (mg/L)	SD TSS (mg/L)	Average DO (mg/L)	SD DO (mg/L)
Gila	G1	Gila at Birds Sanctuary	1336	7	8981	0.001	0.006	310.26	587.40	7.44	1.69
	G2	Gila near Gila	1429	7	6007	0.005	0.006	99.84	164.12	7.27	0.89
	G3	Gila at forks union	1677	7	4898	0.001	0.005	258.77	371.90	8.21	0.96
	G4	East Fork of the Gila	1727	6	3246	0.009	0.007	42.60	25.40		
	G5	Middle Fork of the Gila	1716	6	1107	0.002	0.006	1681.36	4551.87	8.53	1.18
	G6	West Fork of the Gila	1757	5	345	0.01	0.008	22.94	23.98	7.90	2.69
	G7	Mogollon Creek	1874	4	132	0.026	0.11	3.15	2.30		
	G8	West Fork of the Mogollon	1836	3	43	0.036	0.12	4.14	4.10	9.74	1.60
	G9	Rain Creek	1810	3	44	0.022	0.11	7.17	9.59	8.24	2.26
Thur	T1	Thur near Niederneunform	371	7	1678	0.001	0.051	85.42	25.65	9.58	2.87
	T2	Thur near Bischofszell	467	6	741	0.003	0.062	30.15	9.56	10.16	1.51
	T3	Sitter near Bischofszell	474	6	341	0.003	0.094	26.20	7.45	11.58	1.62
	T4	Sitter near Appenzell	784	5	85	0.012	0.107	9.50	2.57	10.83	0.85
	T5	Necker near Mogelsberg	607	5	89	0.006	0.077	11.79	3.54	10.69	0.95
	T6	Wissbach near Weissbad	831	4	26	0.02	0.155	6.56	1.24	10.55	0.77
	T7	Lutter near Rietbad	937	4	17	0.027	0.107	5.32	0.50	10.12	0.68

TSS total suspended solids, DO dissolved oxygen)

(Molles & Dahm, 1990; Uehlinger, 2000; Acuña & Dahm, 2007). Daily mean discharge data from 1980 to 2010 were used to characterize the flow regime in the previously mentioned gaging stations, aiming to determine differences between study sites in terms of temporal variability and predictability. Seven flow-related variables were calculated: mean annual flow, annual coefficient of variation, maximum 1-day flood discharge, maximum 7-day flood discharge, number of no-flow days per year, flow predictability, and the flow constancy-to-flow predictability ratio (Poff & Ward, 1989). Mean annual flow, maximum 1- and 7-day flood discharge, and number of no-flow days per year were used to characterize the magnitude of flow events, whereas annual coefficient of variation and constancy were used to characterize variation. Flow predictability is a measure of the relative certainty of knowing a discharge value at a particular time, and it results from the sum of two components: constancy and contingency. Constancy is a measure of the degree to which the discharge remains constant, whereas contingency is a measure describing how closely the different discharges correspond to different time periods (Colwell, 1974). Predictability indices developed by Colwell (1974) have been used extensively to estimate environmental predictability in ecological (e.g., Gasith & Resh, 1999; Rolls & Arthington, 2014) and evolutionary (e.g., Burgess & Marshall, 2014) sciences. We used the software Indicators of Hydrologic Alteration (IHA, The Nature Conservancy) (Richter et al., 1996) for the calculation of these flow-related variables.

Biological samples

Benthic macroinvertebrate samples were collected before, during, and after a flood period in each river basin. Thus, sampling campaigns were set from July to November 2006 in the Gila (including the monsoonal rains) and from July to October 2007 in the Thur (including a cluster of floods) (Fig. 1). In the Thur, several flood events occurred throughout the year and samples were taken in a period that had a flood four times higher than the most frequent floods (Fig. 1). In both river basins, samples from July were obtained before the main flood period (BEFORE) and samples from August were collected during the flood period. Samples just after the flood period (AFTER) were collected in October in the Gila and in September in

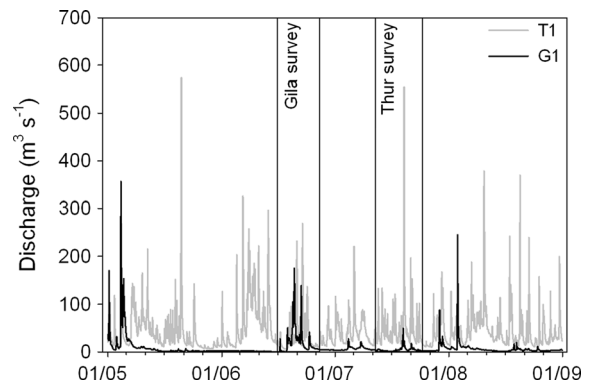


Fig. 1 Discharge in the Gila (site G1) and Thur (site T1) rivers from 1 Jan 2005 to 31 Dec 2008, indicating where the biological survey was done. Data obtained from the U.S. Geological Survey gaging station 09430500 (G1) and the Swiss Federal Office for the Environment gaging station 00136/2044X (T1). Drought periods occurred in the Gila both before (May–mid-June) and after the survey (July–August)

the Thur. Finally, a set of samples was collected 1 month after the end of the flood period (FINAL), thus in November in the Gila and October in the Thur.

Five Hess samples were taken per site (sample area 0.19 m², 250 μm mesh size). Samples were fixed in 70% ethanol and all specimens were sorted in the laboratory and identified at genus level. Merritt & Cummins (1996) was used for the Gila samples, whereas Tachet et al. (2010) was used for the Thur samples. For each genus, we obtained biological trait information from published databases for North American and European macroinvertebrates (Bêche et al., 2006; Statzner et al., 2007; Tachet et al., 2010; Bonada & Dolédec, 2011) (Supplementary Material S2). Both databases include comparable information on 11 biological traits divided into 61 trait categories that consider aspects related to the morphology, behavior, life history, and physiology of macroinvertebrates. As these trait categories summarize all available biological information for each genus, they are potentially applied to all areas where each genus occurs (Statzner et al., 2007; Bonada & Dolédec, 2011). Some of these trait categories were grouped to create a simplified list of traits (e.g., categories a4, a5, a6, and a7 in Tachet et al. (2010) were grouped and named “> 1 to > 8 cm” to refer to large body sizes, Supplementary Material S2). This grouping helped to interpret the results and, at the same time, reduce the phylogenetic relationships among trait categories (Poff et al., 2006). To expand the list of traits that

can be relevant to flood regimes, 15 additional categories were coded for all genera following Tomanova & Usseglio-Polatera (2007) and Bêche et al. (2006). These categories corresponded to the traits: body flexibility, body form, body armoring, and attachment mechanism (codes available by request) (Supplementary Material S2). In all cases, trait categories were coded using the fuzzy coding approach described in Chevenet et al. (1994). This approach accounts for the variability within genus (i.e., among species within a genus along different environmental conditions) and is based on assigning a value from 0 to ≥ 3 (up to 5 for some traits) to each genus and trait category, where 0 indicates no affinity, 1 low affinity, 2 medium affinity, and ≥ 3 strong affinity.

For the purpose of this study, a subset of traits was selected because of their direct relationship to floods (Table 2). Thus, traits such as feeding type were not included because they are not directly related to strategies to withstand, avoid, or recover from floods. The final list included 13 traits and 46 trait categories that were grouped into the 3 types defined by Lytle & Poff (2004): morphological, life-cycle synchronization, and behavioral (Table 2). Morphological traits mainly included trait categories that allow organisms to withstand floods, although some categories allow organisms to avoid floods. Life-cycle synchronization traits included trait categories that allow organisms to avoid floods by synchronizing their life cycles with disturbance events, such as short and multivoltine cycles. Finally, behavioral traits mainly included trait categories that allow organisms to avoid floods by moving to temporary refugia (i.e., hyporheic zone, nearby terrestrial habitats, or distant stable habitats reached by long-distance aerial dispersal) although some categories also might allow organisms to withstand floods (Table 2).

Statistical analyses

Abundance and diversity metrics were computed on the macroinvertebrate averaged samples for each site and sampling period. Diversity metrics for structural composition consisted of genus richness and Simpson diversity, whereas for functional composition consisted of trait richness and Rao's diversity. Trait richness was calculated as the number of trait categories present at each site. Rao's diversity was

computed using the Champely & Chessel (2002) index. This index uses the trait dissimilarity between genera pairs on the abundance matrix. Rao's diversity has been proved to have a high accuracy in the measurement of functional divergence (i.e., the variance of the genera functions and their position in trait space) and to capture more additional independent information than is provided by other functional indices that measure other aspects of functional diversity (i.e., functional richness and evenness; Schleuter et al., 2010). In addition, it is based on the Simpson diversity index, making structural and functional metrics more comparable. A local polynomial regression (LOESS; Cleveland, 1979) was fitted to visualize temporal trends of the different metrics with a degree of smoothing of 1; 95-percentile confidence intervals were also calculated to visualize trend variability. LOESS is a very flexible method that does not require a specific function to fit a model and helps to visualize complex relationships between data.

The effect of the flood period on macroinvertebrate structure and function was evaluated by computing Bray–Curtis dissimilarities between BEFORE and AFTER, and BEFORE and FINAL sampling periods, for each site individually and using raw abundances. Significant differences between the Gila and the Thur basins for these dissimilarity values were tested with a non-parametric ANCOVA, using basin as factor and stream order as covariate to account for the fact that sites were located in different river sections in each basin (i.e., sites within basins cannot be considered totally independent). This analysis tested for significant differences between both basins, considering the equality of non-parametric smooth functions between the response and the covariate (i.e., Bray–Curtis dissimilarity and stream order values, respectively). It is based on an ANOVA-type statistic and uses a wide-bootstrap algorithm, providing a statistic T and a P value. It was preferred over parametric ANCOVA because the response data violated parametric assumptions and were non-linearly related to stream order.

To determine characteristic biological adaptations to floods in each climate region, the frequency of each hypothesized trait category in Table 2 was compared in both basins for the entire study period. First, a trait-by-site matrix was obtained by multiplying the standardized trait-by-genus matrix with the genus-by-site (raw abundance) matrix and re-relativizing within each trait category. This trait-by-site matrix

Table 2 List of biological traits grouped in the three categories described by Lytle & Poff (2004) that directly relate to resistance (endurance) or avoidance of floods

Trait group	Trait	Trait category	Strategy	Mechanism	
Morphological	Body size	Small (≤ 0.25 to 1 cm)	Avoidance	More ability to find refuges (benthic substrate, hyporheos)	
		Large (> 1 to > 8 cm)	Resistance	Higher weight	
	Body flexibility (degrees)	None (< 10)			
		Low (> 10 –45)			
		High (> 45)	Avoidance	More ability to find refuges (benthic substrate, hyporheos)	
	Body form	Streamlined			
		Flattened		Resistance	Less exposed to flow
		Cylindrical			
		Spherical			
	Body armouring	None (soft-bodied)			
		Moderate (sclerotised)			
		Strong (case/shell)	Resistance	Physical resistance	
	Attachment mechanism	Suckers	Resistance	Attachment to the substrate	
Silk gland					
Mineral material case		Resistance	Extra weight		
Anal or tarsal hooks		Resistance	Physical resistance		
No adaptation					
Synchronization	Life cycle duration	≤ 1 year	Avoidance	Short life cycles allow synchronization to annual floods	
		> 1 year			
	Number reproduction cycles	Semivoltine			
		Univoltine	Avoidance	One generation per year allows synchronization to annual floods	
	Multivoltine	Avoidance	Multiple generations per year allow synchronization to annual floods		
Behavioral	Reproduction	Ovoviviparity			
		Free eggs (isolated and clutches)			
		Cemented or fixed eggs (isolated and clutches, epiphytic)			
		Terrestrial (clutches)	Avoidance	Terrestrial oviposition protects offspring	
	Dissemination	Asexual reproduction			
		Aquatic passive			
		Aquatic active			
		Aerial passive	Avoidance	More ability to find refuges (other streams)	
		Aerial active	Avoidance	More ability to find refuges (other streams)	
	Resistance form	Presence (eggs, cocoons, diapause)	Resistance	Form acquired during harsh conditions	
		None			
	Aquatic stages	Egg			
		Larva	Avoidance	Highly mobile stage able to find refuges	
Nymph					
Imago					
Respiration	Aquatic	Resistance	No need to be exposed to high surface flow		
	Aquatic / Terrestrial (plastron type)				
	Terrestrial				

Table 2 continued

Trait group	Trait	Trait category	Strategy	Mechanism
	Locomotion	Flier	Avoidance	More ability to find refuges (other streams)
		Swimmer (surface and underwater)		
		Crawler		
		Burrower and interstitial	Avoidance	More ability to find refuges (hyporheos)
		Temporarily attached	Resistance	Physical resistance
		Permanently attached	Resistance	Physical resistance

The mechanism associated with resistance or avoidance is indicated by a set of trait categories that directly relate to flood adaptations

Table 3 Flow regime characteristics at sites G1 and G7 (Gila) and T1 and T5 (Thur)

Hydrological variable	Gila Basin		Thur Basin	
	G1	G7	T1	T5
Mean annual flow ($\text{m}^3 \text{s}^{-1}$)	6.88	0.83	47.97	3.24
Annual coefficient of variation (%)	2.56	4.04	1.07	1.36
Maximum 1-day flood ($\text{m}^3 \text{s}^{-1}$)	152	31	429	38.64
Maximum 7-day flood ($\text{m}^3 \text{s}^{-1}$)	58	9	198	15.42
Ratio 1-day flood/mean annual flow	22.09	37.35	8.94	11.93
Ratio 7-day flood/mean annual flow	8.43	10.84	4.13	4.76
Number of non-flow days per year (d)	25	0	0	0
Flow predictability	0.41	0.26	0.44	0.37
Constancy: predictability	0.68	0.46	0.84	0.8

Analyses are based on the period 1980–2010 and use data from the U.S. Geological Survey gaging station 09430500 (G1) and 9430600 (G7); and data from the Swiss Federal Office for the Environment gaging stations 00136/2044 (T1) and 00911/2374 (T5)

contained the proportional abundance of each trait category per site and date. Second, trait category frequency was plotted along time and a local polynomial regression (LOESS; Cleveland, 1979) was fitted to visualize temporal trends of each trait category, with 95-percentile confidence intervals. Finally, significant differences between the Gila and the Thur basins for each hypothesized trait category were tested using non-parametric ANCOVA tests, as described above.

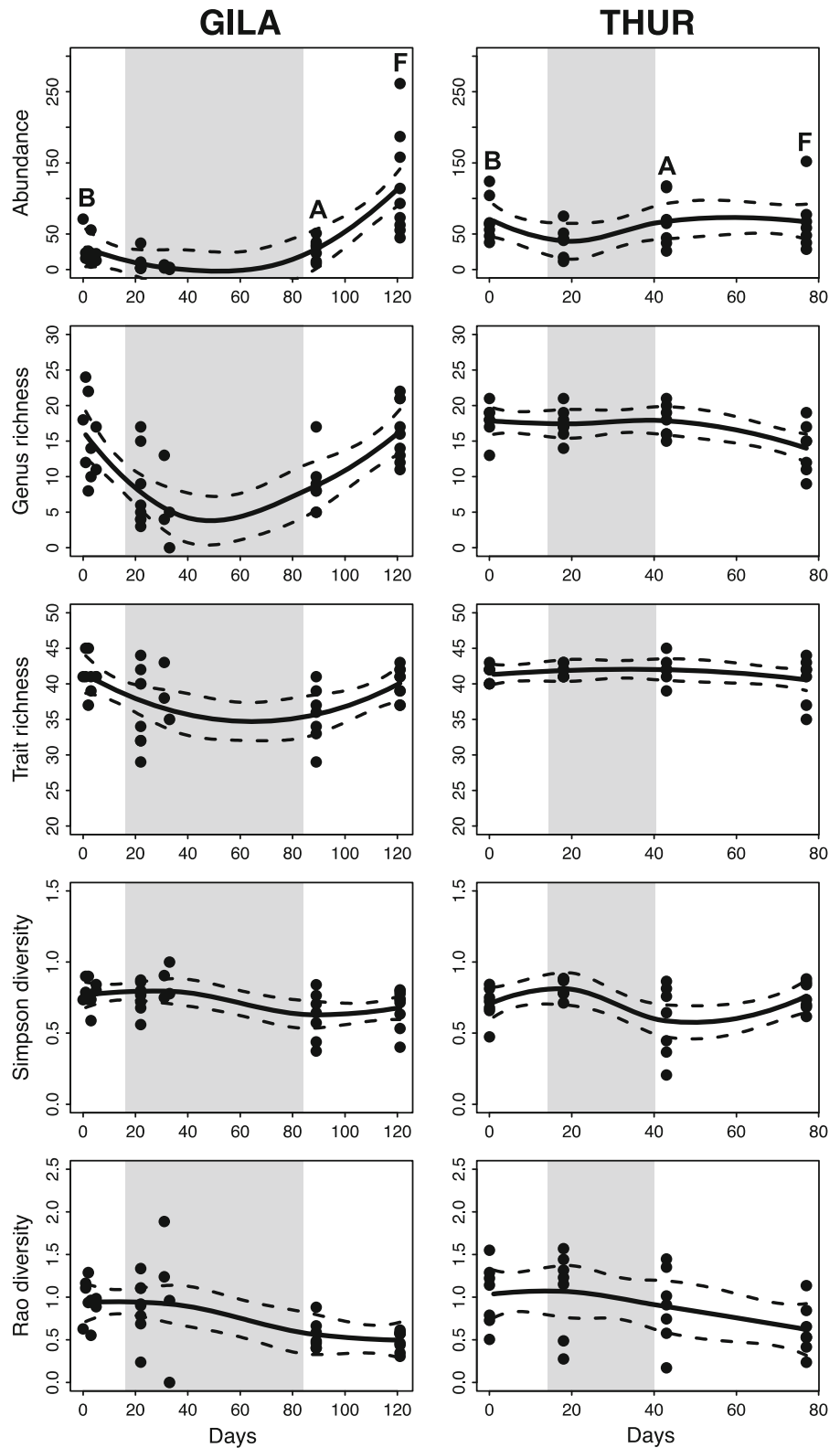
For each analysis, all sites within each basin were considered together because both basins included sites with low, intermediate, and high stream order (3–4, 5–6, and 7, respectively). All statistics regarding hydrological and biological data were computed using R (R core development team, 2013) and the libraries vegan (Oksanen et al., 2013), ade4 (Chessel et al., 2004), and fANCOVA (Wang, 2010).

Results

Flow regime

Discharge in the Gila mainstem (site G1) ranged from 2 to $350 \text{ m}^3 \text{ s}^{-1}$ during the period 2005–2008 (Fig. 1). In June 2006, the monsoon resulted in a rapid increase in rainfall that ended a long drought that had begun in November 2005. The monsoonal rains led to a very wet July 2006, and the rains lasted until late September when a drier period was reestablished over the study area. The 2006 monsoonal rains produced a considerable rise in discharge above the long-term average within the Gila Basin, so that the total discharge at site G1 between July, 1 and September, 30 was 132 hm^3 in 2006, whereas the mean of the past 11 years was 34 hm^3 for the same period. Discharge in the Thur mainstem (site T1) ranged from 11 to $556 \text{ m}^3 \text{ s}^{-1}$ during the period 2005–2008 (Fig. 1), which is within the normal range. During the study period, floods were

Fig. 2 Genus richness, abundance, and trait richness of macroinvertebrates along time for all sites in the Gila and Thur basins with the corresponding LOESS fitting (dashed lines correspond to the 5th and 95th percentiles). Time refers to days after the first sampling date. The gray rectangle indicates the flood period in each basin. *B* samples taken before the flood period, *A* samples taken just after the flood period, *F* final sampling, corresponding to the base flow period



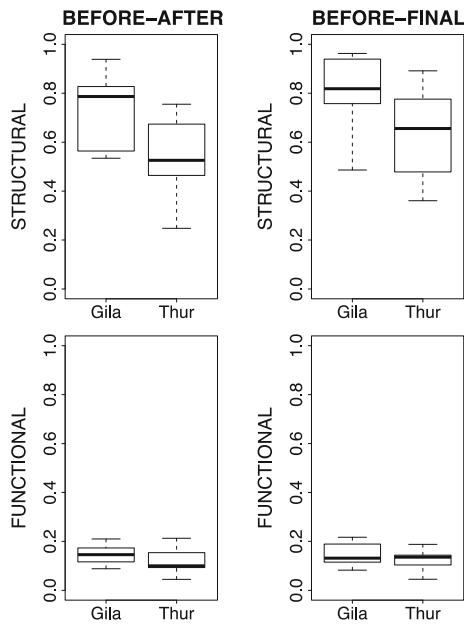


Fig. 3 Bray–Curtis distances measuring structural and functional dissimilarity for the comparison before–after the flood period and before–final the flood period. Boxplots represent results for all sites in each basin

more frequent in the Thur than in the Gila and had a higher absolute magnitude (Fig. 1).

Predictability at the basin outlets (sites T1 and G1) was similar in the Thur and Gila basins, and there was a decrease for smaller drainage areas in both basins (sites G7 and T5; Table 3). The relationship between predictability and drainage area was more pronounced at the Gila Basin, which experienced major changes from sites G1 to G7. Regarding the ratio of constancy: predictability, major differences existed between the Thur and the Gila, with the Thur showing values around 0.8 and the Gila around 0.5 (Table 3). Furthermore, the differences between sites within each basin were more pronounced in the Gila, with values of constancy: predictability decreasing for smaller drainage areas. In contrast, there were no major changes of this ratio among sites within the Thur. Overall, flow in the Thur was predictable (high constancy), aseasonal, and with a high flood frequency, whereas in the Gila flow was also predictable (although with lower constancy), seasonal, and had a low annual flood frequency.

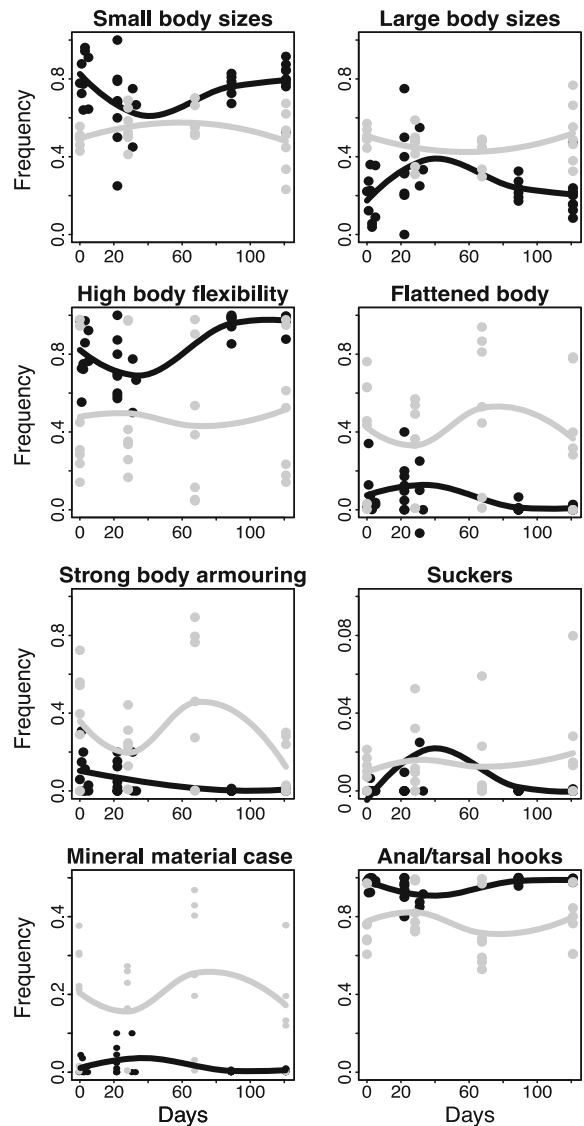


Fig. 4 Proportion of individuals (range 0–1) having each morphological trait category along time for all sites in the Gila and Thur basins with the corresponding LOESS fitting. Time refers to days after the first sampling date. The black line corresponds to the Gila whereas the gray line corresponds to the Thur. See Table 2 for the hypothesized mechanisms of resistance and/or avoidance of floods

Structural and trait composition

Temporal trends in abundance and all diversity metrics were more distinct for the Gila than for the Thur (Fig. 2). In the Gila, abundance was higher during the FINAL period, whereas it remained constant BEFORE, AFTER, and during the flood period.

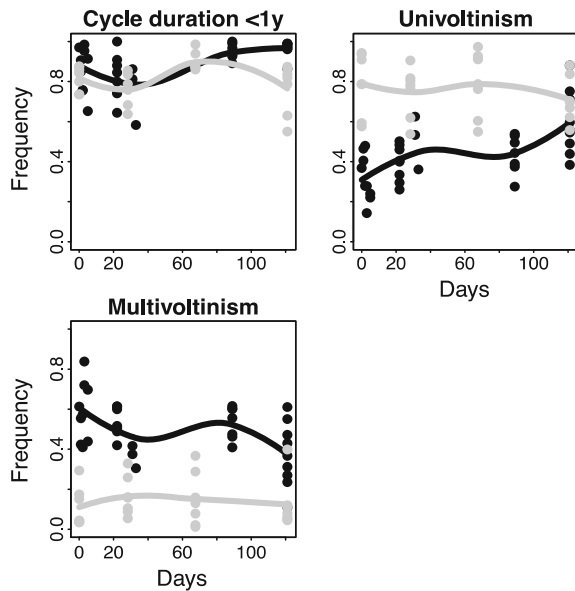


Fig. 5 Proportion of individuals (range 0–1) having each life-cycle synchronization trait category along time for all sites in the Gila and Thur basins with the corresponding LOESS fitting. Time refers to days after the first sampling date. The black line corresponds to the Gila, whereas the gray line corresponds to the Thur. See Table 2 for the hypothesized mechanisms of resistance/avoidance to flood

In the Thur, abundance decreased slightly during the flood period. The flood period resulted in a decrease in genus and trait richness in the Gila but was unaffected in the Thur. Diversity metrics decreased over time in both basins, specifically Rao diversity (Fig. 2). Structural composition BEFORE and AFTER the flood period was more similar for the Thur than for the Gila albeit non-significant (non-parametric ANCOVA, $T = 0.201$, $P = 0.602$; Fig. 3) and a similar, but also non-significant, trend was observed when comparing BEFORE and FINAL samples (non-parametric ANCOVA, $T = 0.236$, $P = 0.572$). Trait composition was very similar when comparing BEFORE and AFTER, and BEFORE and FINAL samples for both basins. However, the Gila had slightly higher, albeit non-significant, differences among sampling periods (BEFORE–AFTER: non-parametric ANCOVA, $T = 0.009$, $P = 0.616$; BEFORE–FINAL: non-parametric ANCOVA, $T = 0.008$, $P = 0.567$).

Overall, the presence of morphological traits that confer resistance to floods was more common in the Thur (e.g., large body sizes), whereas the presence of life-cycle synchronization and behavioral traits

conferring resilience or resistance were more common in the Gila (e.g., cycle duration < 1 year, temporary attachment) (Figs. 4, 5, 6, Table 4).

Regarding morphological traits, the Thur, compared to the Gila, had a higher proportion of individuals with large body sizes, flattened bodies, strong body armoring, suckers, and mineral material cases (Fig. 4, Table 4). In contrast, the Gila had a higher dominance of individuals with small body sizes, high body flexibility, and anal/tarsal hooks than the Thur. Some of these trait categories also varied temporally. In the Thur, organisms with strong armoring and mineral material cases were more frequent before and just after the flood period, whereas the proportion of organisms with anal/tarsal hooks decreased. In the Gila, small organisms with high body flexibility increased after the flood period, whereas organisms with suckers decreased (Fig. 4).

Concerning life-cycle synchronization traits, the Gila had, in comparison with the Thur, a higher proportion of organisms with multivoltine cycles and a slightly but significantly higher number of organisms with short life cycles (Fig. 5, Table 4). In contrast, univoltine cycles were significantly more frequent in the Thur than in the Gila. For both basins, organisms with short life cycle duration increased after the flood period (Fig. 5).

Finally, regarding behavioral traits, the Thur was characterized by a higher proportion of organisms with aerial passive dispersion (Fig. 6, Table 4). Organisms that were permanently attached were also more common in the Thur albeit not significant after accounting for the stream order. In contrast, the Gila exhibits a community formed by a higher proportion of temporarily attached organisms that lay terrestrial eggs in clutches, having various resistance forms or aquatic larval stage. They can also disperse aerially actively or burrow to interstices (Table 4). Most of these traits also varied with time. Fliers decreased just after the flood period in both basins but reappeared at the end of the study period. Despite their low proportion, permanently attached organisms increased after the flood period in the Thur, whereas in the Gila they remained absent. In the Gila, temporarily attached organisms disappeared after the flood period (Fig. 6).

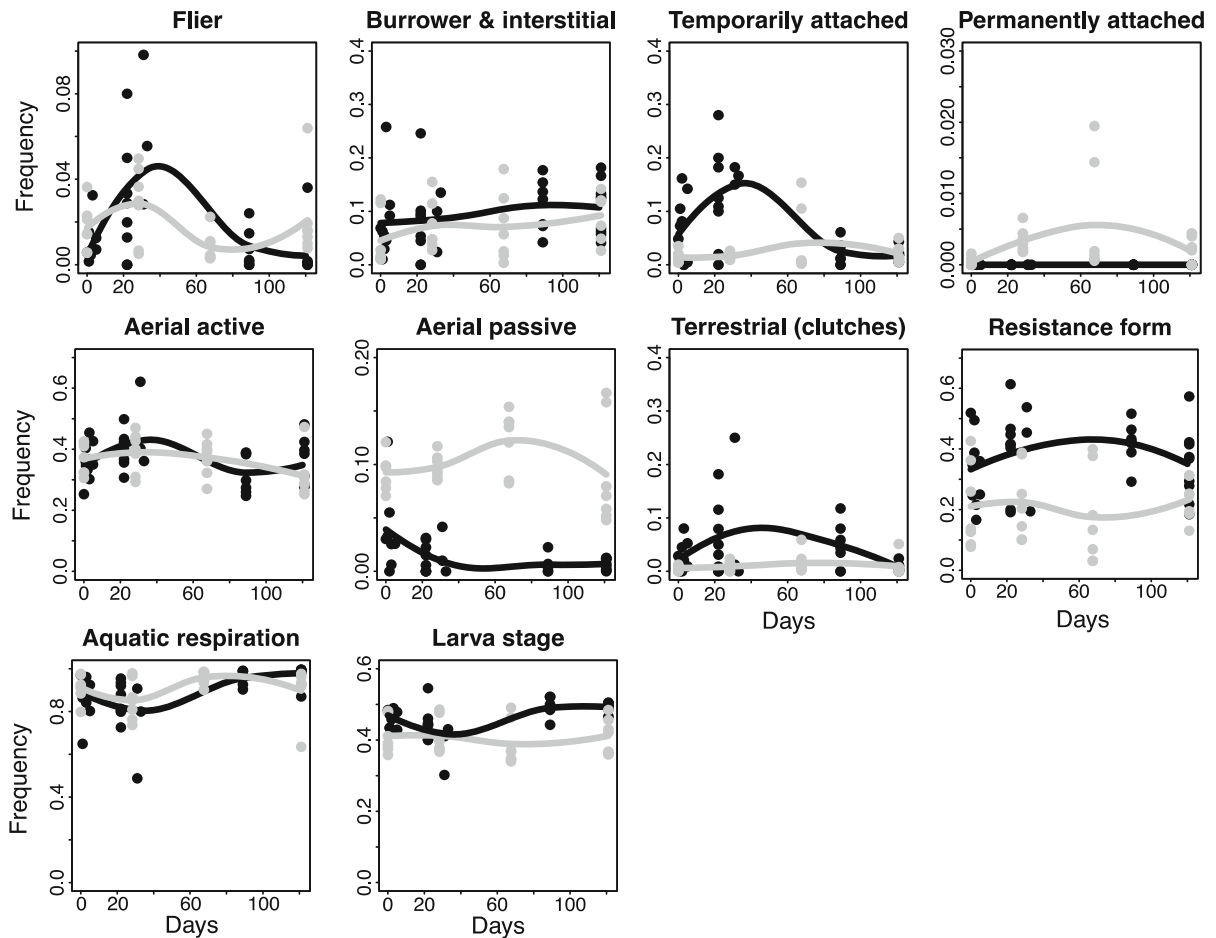


Fig. 6 Proportion of individuals (range 0–1) having each behavioral trait category along time for all sites in the Gila and Thur basins with the corresponding LOESS fitting. Time refers to days after the first sampling date. The black line

corresponds to the Gila whereas the gray line corresponds to the Thur. See Table 2 for the hypothesized mechanisms of resistance/avoidance to flood

Discussion

The responses of macroinvertebrates to the two contrasting flow regimes differed in structural and functional metrics and composition. Immediate flood effects were much more evident for the Gila than for the Thur. Structural and functional richness decreased slightly after the flood period in the Gila, whereas all metrics remained unaffected in the Thur. Similarly, the flood period had greater effects on the structural and trait composition in the Gila than in the Thur. In contrast to other studies that highlighted the fatal effects of floods by drastically reducing abundance and diversity (Robinson et al., 2004), our results show that floods had only slight effects on these metrics and

suggest that the Gila had higher resilience than the Thur.

Resistance and avoidance strategies

Biological adaptations appeared related to the flow regime of each climatic region. As expected, synchronization strategies were more typical in the Gila and morphological trait categories that enable resistance to floods were more common and stable in the Thur, lasting from the pre-flood sampling to at least a month after the flood period. Therefore, our results support the general predictions made by Lytle & Poff (2004) for these two types of traits in the sampled basins, indicating that macroinvertebrate communities have

Table 4 Non-parametric ANCOVA tests between the Gila and the Thur for each of the hypothesized trait categories in Table 2

Trait group	Trait category	Strategy	Mean-Gila	SE-Gila	mean-Thur	SE-Thur	<i>T</i>	<i>P</i> value	
Morphological	Small body sizes	Avoidance	0.747	0.025	0.525	0.019	0.011	0.005	**
	Large body sizes	Resistance	0.252	0.025	0.475	0.019	0.011	0.005	**
	High body flexibility	Avoidance	0.846	0.026	0.480	0.064	0.031	0.005	**
	Flattened body	Resistance	0.061	0.016	0.410	0.057	0.025	0.005	**
	Strong body armouring	Resistance	0.047	0.013	0.284	0.052	0.012	0.012	*
	Suckers	Resistance	0.004	0.003	0.014	0.004	< 0.001	0.044	*
	Mineral material case	Resistance	0.013	0.004	0.197	0.028	0.007	0.005	**
	Anal/tarsal hooks	Resistance	0.964	0.008	0.778	0.028	0.007	0.005	**
Synchronization	Cycle duration < 1y	Avoidance	0.887	0.019	0.810	0.018	0.002	0.035	*
	Univoltinism	Avoidance	0.443	0.026	0.759	0.026	0.021	0.005	**
	Multivoltinism	Avoidance	0.492	0.024	0.138	0.021	0.025	0.005	**
Behavioral	Flier	Avoidance	0.016	0.004	0.019	0.003	< 0.001	0.254	
	Burrower and interstitial	Avoidance	0.093	0.011	0.070	0.010	< 0.001	0.015	*
	Temporarily attached	Resistance	0.068	0.012	0.023	0.006	< 0.001	0.029	*
	Permanently attached	Resistance	0	0	0.003	0.001	< 0.001	0.069	
	Aerial active	Avoidance	0.366	0.013	0.361	0.013	0.001	0.025	*
	Aerial passive	Avoidance	0.016	0.004	0.101	0.006	0.001	0.005	**
	Terrestrial (clutches)	Avoidance	0.038	0.009	0.010	0.003	< 0.001	0.019	*
	Resistance form	Resistance	0.372	0.02	0.211	0.023	0.005	0.005	**
	Aquatic respiration	Resistance	0.901	0.018	0.906	0.016	< 0.001	0.074	
	Larva stage	Avoidance	0.464	0.007	0.406	0.009	< 0.001	0.005	**

Trait categories are grouped into trait groups and classified into resistance/avoidance strategies. See Table 2 rationale behind resistance/avoidance strategies. The mean of each trait category (the mean proportion of the number of individuals, ranging from 0 to 1) and the standard error is presented separately for each basin

* Significant *P* value at < 0.05; ** Significant *P* value at < 0.01; any trait category was significant according to a Bonferroni correction

evolved adaptations in response to disturbance regimes. Flow is most likely an agent of natural selection and, together with substrate stability and the presence of refugia, represents the three key variables governing macroinvertebrate communities in river ecosystems (e.g., Fleituch, 2003; Death, 2008).

However, and in contrast to our hypothesis, a higher proportion of behavioral traits conferring resistance or resilience were more commonly found in the Gila than in the Thur. Most of these significant traits are known to be also common strategies to resist or avoid droughts even in highly predictable climates such as the Mediterranean (Bonada et al., 2007; Hershkovitz & Gasith, 2013). Bonada et al. (2007) showed that these strategies were significantly more frequent in Mediterranean than in temperate climates such as that found in the Thur. Therefore, the behavioral strategies observed in the Gila could be more related to droughts

than to floods. In fact, most of these traits increased in proportion both before and after the flood period in the Gila, corresponding to the end and beginning of drought period (Figs. 1, 6).

In both basins, floods affected organisms differently depending on their traits. In the Gila, small organisms with high body flexibility were reduced during the flood period but increased afterwards, showing their potential ability to find nearby refugia when necessary (Robinson et al., 2004). Besides morphological adaptations, the Gila also had a higher proportion of behavioral traits that enable organisms to avoid floods, such as the presence of larvae able to find refugia or organisms laying terrestrial eggs. This last trait category together with the higher dominance of organisms with resistance forms, however, might be related to the drought period that follows the flood period in the Gila, as these adaptations are

characteristic of temporary rivers (Bonada et al., 2007). Life cycles appeared to be highly synchronized with the flood period in the Gila. Thus, during the pre-flood conditions, multivoltine strategies and short life cycles were dominant, allowing the macroinvertebrates to develop rapidly and escape to terrestrial habitats as adults before the flood period. In addition, the increase of the proportion of organisms with univoltine life cycles after the flood period in the Gila would indicate that the multivoltine taxa emerged before the flood period, reinforcing the idea that resilience strategies are important in the Gila. In this case, the first flood of the flood period is the primary selective force driving emergence patterns, although subsequent floods may be important for oviposition timing as well (Lytle, 2002; Robinson et al., 2004).

Compared to the Gila, the Thur presented a very different flood regime. It was characterized by regular and recurrent (high constancy) aseasonal floods, which resulted in frequently disturbed conditions. In fact, although a period of higher floods was identified (i.e., the period considered in this study), floods may occur throughout the year (Uehlinger, 2000). Macroinvertebrate communities in these streams seem to be continuously impacted by these frequent floods that also truncate their development. In studies of more spaced floods, low diversity and abundance have been observed, as well as the capacity for macroinvertebrate communities to recover within a month following flood disturbance (Robinson et al., 2004). In our study, the Thur experienced floods 1 month prior to our pre-flood sampling. Consequently, the effects of the studied flood period were masked because pre-flood conditions already resulted in a potentially impacted macroinvertebrate community BEFORE (Lytle, 2002). As a consequence of these frequent floods in the Thur, macroinvertebrate life cycles do not appear to be synchronized with the flood periods, as evidenced by the presence of univoltine macroinvertebrates that could only be present under recurrent and unpredictable floods if other strategies, such as morphological adaptations that enable resistance (e.g., attachment by suckers, flattened bodies), were present. Thus, many strategies to withstand floods were frequent in the Thur, comprising characteristic morphological and few behavioral adaptations, such as being permanently attached or having an aquatic respiration. These strategies would explain the

semivoltine life cycles found for large predatory stoneflies in the Thur (Imhof, 1994).

Implications for flow regime alterations

The types of adaptations to flow regimes examined in this study (morphological, behavioral, and life-cycle synchronization) are unlikely to respond rapidly to flow regime changes. Aquatic species have evolved these adaptations to natural flow regimes and their survival may therefore be compromised because natural flow regimes are changing faster than the evolutionary rate. Although several studies have found that microevolutionary changes to temperature occur in many organisms, including aquatic ones (Skelly et al., 2007), no studies have been done so far on microevolution and flow regime alterations. Obviously, a streamlined macroinvertebrate will not be able to acquire a spherical shape in a few generations and, although life cycle changes are more likely to occur by changing emergence timing, they are more dependent on temperature changes (degree days) than on flow alterations. For example, the same species could be multivoltine at high temperatures and univoltine at low temperatures regardless of the flow regime (Bonada et al., 2007). Therefore, alterations of natural flow regimes are expected to be dramatic for aquatic organisms and most would be forced to move to more suitable areas (Heino et al., 2009). The match that we found between flow regimes and the strategies adopted by macroinvertebrates allows us to better understand through which mechanisms macroinvertebrates could be affected. However, evaluating the effects of flow regime alterations on traits is always a challenge. Organisms are characterized by a set of traits and adaptation to a particular flow regime (or the environment in general) can be achieved through several combinations of traits (and tradeoffs) (Verberk et al., 2013).

Forecasted future flow regimes for arid and semi-arid regions differ from those for more mesic temperate regions. In the arid and semi-arid regions in North America with tropical influences, spring flood pulses associated with snow melt will be weaker and occur earlier (Cook & Seager, 2013; Gutzler, 2013), bringing greater aridity to the region (Seager et al., 2008). Therefore, and according to the results from the Gila, a mismatch between flow regimes and life-cycle synchronization of the organisms living in these arid and

semi-arid regions could be expected. However, despite the potential for a dramatic reduction in populations of flood-synchronized species, the expected increase in temperature (Seager et al., 2008) together with the multivoltine life cycles of these species, might compensate these losses.

Models for temperate oceanic regions in Europe, where the Thur is located, forecast alterations in the magnitude and timing of flows. Summer flows will be reduced, winter flows will slightly increase, and flood peaks will be advanced because the snowpack will be reduced and snowmelt will start earlier (Schneider et al., 2012). Under these conditions, predicted flow alterations will have more certain and less dramatic consequences in the Thur than in the Gila. Our results showed that resistance strategies to floods were most frequently encountered in the Thur. A slight reduction in summer flows and an advance in the flood period thus will have minimal effects on the macroinvertebrate community because the community already consists of taxa adapted to frequent floods throughout the year.

Flow regime alterations, together with temperature shifts, will be determinant for aquatic organisms that will be forced to rapidly adapt through changes in distribution patterns and in microevolutionary processes (Filipe et al., 2013). Our results show that the effects of flow alterations will ultimately depend on the adaptation of the organisms to current flow regimes and particular alterations in the frequency, predictability, timing, and magnitude of the flow regimes. Therefore, our results support predictions made by Lytle & Poff (2004) suggesting that changes in timing will be more exacerbated in climate regions with life-cycle synchronization to flow regimes, such as in the Gila, and will be less dramatic in climate regions where other adaptations are the rule.

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