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Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence

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Abstract: In naturally disturbed systems, harsh environmental conditions act as filters on the regional species pool, restricting the number of taxa able to form a local community to those with traits promoting resistance or resilience. Thus, communities in highly disturbed ecosystems may be less sensitive to a given disturbance than those in less disturbed ecosystems. We explored this idea by examining the response of aquatic invertebrate communities to flow intermittence in gravel-bed, braided rivers (BRs). Flow intermittence is considered a major driver of communities in rivers, but its influence on communities in BRs, which are recognized as naturally highly disturbed environments, is relatively unexplored. We used a multisite Before-After-Control-Impact (BACI) design to quantify the effects of drying events of different durations (moderate: 2–3 wk, severe: 1–3 mo) on invertebrate communities in 8 BRs in southeastern France. As predicted, no effects of flow intermittence were detected 1 to 4 mo after flow resumption on taxonomic richness, composition, or functional diversity of communities facing moderate drying events. Communities subjected to severe drying events were similar to those in perennial reaches as few as 19 d after flow resumption. Moreover, communities showed functional redundancy and no loss of functional diversity after drying events. These results differ from those of studies in other river systems, where persistent effects of flow intermittence on communities generally have been found, and highlight the need for cross-system comparisons that explore the effects of drying on communities. Identifying the processes (e.g., niche selection, cotolerance) and habitat features (e.g., hyporheic zone refugia) that promote community resilience in BRs will advance our understanding of how anthropogenic stressors and climate change may affect communities in freshwater ecosystems.

Key words: resistance, resilience, recovery, co-tolerance, hyporheic zone, alluvial rivers, BACI design

One pervasive goal of community ecology is to identify processes that determine variation in taxonomic richness, composition, and abundance of communities (Leibold et al. 2004, Vellend 2010). Disentangling the different processes involved in community assembly and the spatiotemporal scales at which they operate and interact is essential to predict the responses of communities to future environmental changes (Götzenberger et al. 2012). At broad scales, evolutionary processes, climate (e.g., precipitation and temperature regime), and historical events act together to determine a regional species pool (Poff et al. 1997). Furthermore, the potential for taxa in the regional species pool to form a local community is a function of a series of selective filters, including the abiotic environment and biotic interactions, which operate over multiple nested habitat levels (Leibold et al. 2004). Thus, the persistence of a taxon

in a local community depends on whether it possesses a combination of traits (life history, morphological, mobility, and ecological) to pass through multiple habitat filters (niche theory; Whittaker et al. 1973).

In naturally disturbed ecosystems, abiotic environmental conditions border on extreme values and are often unstable or stochastic, so fewer taxa from the regional species pool are available to form a local community (Chase 2007, Lepori and Malmqvist 2009). Therefore, taxa rely on combinations of traits (i.e., strategies sensu Southwood 1988) that promote resistance, resilience, or both to disturbances (Stanley et al. 1994, Fritz and Dodds 2004). Resistance is the capacity of a taxon, community, or ecosystem to persist unchanged through a disturbance, whereas resilience is its capacity to recover (return to predisturbance levels or similarity with undisturbed sites) after the disturbance

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(Stanley et al. 1994, Datry et al. 2014a). Resistance strategies generally include physiological and morphological traits (e.g., resistance to heat or to shear stress), whereas resilience strategies are related to movement/dispersal from sources of colonization (Williams 2006). Furthermore, traits that enhance resistance and resilience to one type of disturbance also can increase tolerance to other disturbances, a concept termed positive cotolerance (Vinebrooke et al. 2004). Consequently, communities in very disturbed ecosystems, where multiple and disparate disturbances occur with relatively high frequency, may show a limited response to a discrete disturbance (Vinebrooke et al. 2004, Côté and Darling 2010).

Gravel-bed, braided rivers (BRs) provide an archetype of naturally highly disturbed ecosystems, making them good systems in which to explore the response of communities to disturbances (Tockner et al. 2010). In BRs, multiple disturbances occur frequently in the form of predictable and stochastic floods and drying events (Arscott et al. 2002, Tockner et al. 2010). Habitat turnover rates are extremely high in BRs. For instance, 60% of the aquatic habitat can change to terrestrial habitat in <2.5 y because of bed scouring and channel movements (van der Nat et al. 2003). During periods of low flow, most, if not all, of the braided channel network becomes dry in areas of large-scale downwelling, where surface water infiltrates into the groundwater. In contrast, areas of large-scale upwelling generally have perennial surface flow (Malard et al. 2003, Doering et al. 2007). Despite the physically harsh environmental conditions, BRs harbor, at the catchment scale, rich invertebrate communities composed of taxa with resistance and resilience strategies (e.g., Arscott et al. 2002, Gray and Harding 2007).

BRs experience multiple natural disturbances, but most research has focused on the effects of floods (e.g., Scrimgeour et al. 1988, Olsen and Townsend 2005), leaving the response of communities to channel drying relatively unexplored (but see Sagar 1983, Fowler 2004). Flow intermittence (i.e., the periodic loss of surface water in river channels) is considered a major driver of river communities and can induce declines in taxonomic richness and shifts in community composition and functional diversity that may persist for several months to years after flow resumption (e.g., Arscott et al. 2010, Bogan et al. 2013, Datry et al. 2014a). However, communities in BRs may be less affected by drying than those from other intermittent rivers because their constituent taxa possess traits that promote resistance and resilience. For example, invertebrate taxa in habitats subject to frequent floods and bed scouring possess traits, such as small body size and high mobility, that allow them to navigate interstitial spaces in river beds to escape harsh surface flows (Townsend and Hildrew 1994, Statzner and Bêche 2010). These same traits allow taxa in intermittent reaches to recover quickly after

drying by migrating from nearby drying refuges (Bonada et al. 2006, Robson et al. 2011), including the underlying hyporheic zone (i.e., saturated interstitial areas beneath the river bed; White 1993), which is expansive in BRs (Capderrey et al. 2013). However, the factors that promote the resistance and resilience of communities may be curtailed by the duration or severity of drying events, which is considered one of the main flow-regime components driving the response of communities (e.g., Poff et al. 1997, Lytle and Poff 2004). Severe drying events often are associated with greater distance to sources of colonization (e.g., Larned et al. 2011) and dry hyporheic sediments (e.g., Boulton 2003, Datry 2012). Therefore, the effects of channel drying on communities may differ depending on the duration of drying events (Lake 2003, Datry et al. 2014a).

We addressed the effects of flow intermittence on taxonomic richness, composition, and functional diversity of aquatic invertebrate communities across 8 BRs in southeastern France. We used a multisite Before–After–Control–Impact design to quantify the effects of drying events of different durations (moderate: 2–3 wk, severe: 1–3 mo) on these communities. We predicted that moderate drying events would have no detectable effects on communities because taxa are frequently exposed to multiple disturbances and, therefore, have strategies that promote their resistance and resilience. Moreover, we predicted that severe drying events would alter communities because resistance and resilience strategies of taxa will be less effective as channel drying becomes exacerbated and the availability of refuges, including saturated hyporheic sediments, decreases with increased drying duration.

METHODS

Braided rivers and study reaches

We studied 8 BRs in southeastern France, a region that contains a high concentration of BRs in the Alps (Fig. 1, Table 1; Piégay et al. 2009). These rivers are influenced or dominated by a Mediterranean climate, including mild, rainy springs and hot, dry summers (Piégay et al. 2009). Flow regimes in Mediterranean rivers are characterized by floods and drying events that are more stochastic, frequent, and intense than those in rivers in temperate climate zones (Bonada et al. 2007). For example, in addition to frequent summer drying events, BRs in this region had up to 28 overbank flood events between 1990 and 2000 (Belletti et al. 2014).

The focal BRs are 17 to 74 km (mean \pm SD, 39 ± 21 km) in length, with catchment areas from 112 and 612 km² (326 ± 171 km²), and have mean annual discharge from 1.3 to 3.2 m³/s (2.1 ± 0.7 m³/s) (Table 1). For each river, we selected an intermittent reach that underwent drying during the study period (May–November 2011) and a

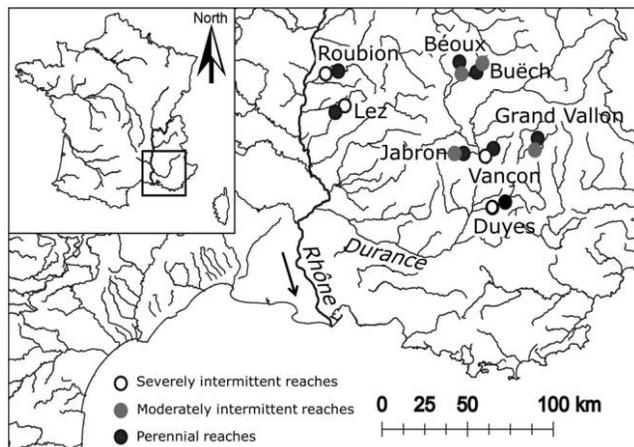


Figure 1. Location of the intermittent and perennial reaches across 8 gravel-bed, braided rivers in southeastern France.

nearby perennial reach that flowed throughout the study period (Fig. 1, Table 1). We selected reaches based on observations from previous studies (Capderrey et al. 2013), aerial photographs (www.geoportail.fr), and preliminary field visits. Intermittent reaches were in downwelling areas, typically characterized by a wide and active braided band and a large valley bottom (Capderrey et al. 2013). At these reaches, surface water was completely absent during drying events and disconnected pools persisted only for ≤ 1 –2 d because of high hydraulic conductivity of the river bed.

Perennial reaches were upstream ($n = 3$) or downstream ($n = 5$) of the intermittent reaches (mean distance = 2.4 ± 1.8 km; Table 1) in areas with narrow active braided channels and valley bottoms (Fig. 1). In all rivers, segments with perennial flow were present upstream of intermittent study reaches. The active braided channel was 12–278 m wide (78 ± 65 m), whereas the mean wetted width of study reaches, measured before and after drying, was 1–6 m (Table 1).

Quantification of flow intermittence

At each reach, we continuously monitored the presence or absence of surface water from 4 May to 1 December 2011 using Onset Hobo[®] water state loggers (Intermountain Environmental, Inc., Logan, Utah). The loggers consisted of a water state data logger, submersible case, coated cable (length = 10 m), and water presence sensor. A detailed description of the loggers and their installation are provided in Appendix S1.

Invertebrate community sampling

We collected benthic invertebrates from each reach in 2 sampling periods, spring (4–12 May 2011) and autumn (21–30 November 2011), which occurred before (≥ 5 d) and after (≥ 19 d) summer drying events, respectively. At each reach, we selected 3 runs to minimize between-habitat variability among reaches, including the 1–3 runs at which loggers had been installed. Within each run, we

Table 1. Mean annual discharge, river length, distance between reaches, active channel width, and reach width across 8 braided rivers that experienced moderate or severe drying events.

Drying class	River	Reach type	Catchment area (km ²)	Annual discharge (m ³ /s)	River length (km)	Distance between reaches (km)	Elevation (m)	Active channel width (m)	Wetted reach width (m)
Moderate	Bèoux	Intermittent	389	–	17.3	2.2	874	141	4–5
		Perennial					923	31	4–5
	Buëch	Intermittent	389	2.1	44.5	2.8	895	98	3–5
		Perennial					869	70	3–5
	Grand Vallon	Intermittent	332	–	19.2	0.7	638	42	1–2
		Perennial					626	58	1–2
Jabron	Intermittent	205	3.2	36.5	5.8	482	278	5–6	
	Perennial					462	61	5–6	
Severe	Duyes	Intermittent	124	1.9	25.2	1.8	396	37	2–5
		Perennial					515	47	2–5
	Lez	Intermittent	445	1.3	73.5	4.0	208	77	3–4
		Perennial					178	77	2–3
	Roubion	Intermittent	612	1.9	66.0	1.2	190	30	2–5
		Perennial					187	12	2–5
Vançon	Intermittent	112	–	30.2	0.3	466	140	2–5	
	Perennial					468	51	3–5	

randomly collected 2 benthic invertebrate samples with a Hess sampler (diameter = 40 cm, area = 0.125 m², 200- μ m mesh) for a total of 192 samples (6 samples/reach \times 2 reaches/river \times 8 rivers \times 2 sampling periods). We preserved samples with 96% ethanol and counted and identified all invertebrates to the lowest practical taxonomic level in the laboratory. We identified all mollusks and most insects to the level of genus and crustaceans, annelids, and mites to the level of genus, family, or order.

Data analysis

Quantification of flow intermittence across reaches For each run where loggers were installed, we quantified flow intermittence based on total number (n , events), total duration (D_{total}), mean duration (D_{mean}), and maximum duration (D_{max}) of drying events during the period of record. We also calculated the length of time before the first drying event (T_{before}) and the length of time after the last drying event (T_{after}), relative to the date that invertebrate samples were collected in spring and autumn, respectively. These data confirmed our initial assignment of reaches into intermittent and perennial reach types. We then assigned intermittent reaches into 2 drying classes: moderate drying ($n = 4$ reaches) when D_{max} was <1 mo and severe drying ($n = 4$ reaches) when D_{max} was >1 mo. We chose D_{max} to categorize drying severity because it represents the longest continuous drying event experienced by aquatic invertebrate communities during the study period, which sometimes included multiple brief periods (1–2 d) of flow resumption. These 2 drying classes represent drying events in the focal study and do not necessarily match the severity of drying in other types of intermittent rivers (i.e., desert, karstic, polar), where drying events can be longer.

Effects of flow intermittence on taxonomic richness and composition of invertebrate communities

We described invertebrate communities at each reach and for each period in terms of taxonomic richness, density (individuals [ind]/m²), and the proportions (% relative abundance) of EPT (Ephemeroptera, Plecoptera, Trichoptera) and OCHD (Odonata, Coleoptera, Heteroptera, Diptera). The latter 2 metrics commonly change in response to drying events because a shift occurs from lotic (mostly preferred by EPT) to lentic (mostly preferred by OCHD) habitat types, which usually precedes complete channel drying (e.g., Bonada et al. 2006, Williams 2006). These metrics were used as dependent variables in linear mixed-effects models with Gaussian error distribution. Density was $\log_{10}(x + 1)$ -transformed, and proportion data were $\arcsin\sqrt{x}$ -transformed to meet the assumptions of parametric analysis. For each dependent variable, models included 2 sampling periods (before and after drying events), 2 reach types (intermit-

tent, perennial), and the interaction term (reach type \times sampling period) as categorical fixed factors and river as a random factor (Bolker et al. 2009). We used the significance of the interaction term ($p < 0.05$) to identify a significant effect of drying. We analyzed invertebrate data from moderate ($n = 4$) and severe ($n = 4$) reaches separately. We constructed all linear mixed-effects models using R software (version 2.8.1; R Project for Statistical Computing, Vienna, Austria) *nlme* package (Pinheiro et al. 2014). We calculated effect size and 95% confidence intervals for each richness and composition metric across reach types, regardless of sampling period, for both drying classes (Table S1 in Appendix S2).

We used Adonis, a permutational multivariate analysis of variances (Anderson 2001), to test for the effects of reach type, sampling period, and their interaction on multivariate taxonomic composition. Adonis returns a R^2 statistic that is a measure of separation among groups (0 indicates complete mixing and 1 represents full separation) according to Bray–Curtis dissimilarity values calculated using $\log_{10}(x + 1)$ -transformed invertebrate abundance and a p -value estimated by repeated permutations ($n = 999$) of the data. The design included 2 sampling periods (before, after) and 2 reach types (intermittent, perennial) and used river as random factor. We performed Adonis separately for both drying classes.

We used nonmetric multidimensional scaling (NMDS) to visualize compositional changes in invertebrate communities among reach types and sampling periods. First, we calculated dissimilarity matrices by means of the Bray–Curtis dissimilarity index from the mean $\log_{10}(x + 1)$ -transformed invertebrate abundance by sampling period and reach type. Second, we used Procrustes to display spatial ordinations (between reach) across before and after sampling periods. Procrustes uses uniform scaling (expansion or contraction) and rotation to minimize the squared differences between 2 ordinations (Peres-Neto and Jackson 2001). Within each drying class, the ordinations of all reaches according to their taxonomic composition are shown simultaneously, and for each reach, arrows join their respective positions between sampling periods. We performed NMDS, Procrustes, and Adonis statistical procedures with functions in the R package *vegan* (Oksanen et al. 2013).

Effects of flow intermittence on functional diversity, trait richness, and composition of invertebrate communities

We compared Rao's quadratic entropy (i.e., functional diversity), trait richness, and composition between sampling periods and reach types. Rao's quadratic entropy is an abundance-weighted metric that measures the mean pairwise dissimilarities of randomly selected taxa in a community as a way of describing the breadth of traits present within a community (Rao 1982). Trait richness is

measured as the total number of traits represented within the community. Generally, these 2 metrics serve as a proxy of the different ecological roles (i.e., functions) that taxa play in an ecosystem and respond to changes in trait composition (Heino 2005). For these metrics, we characterized invertebrate communities based on 61 traits representing 8 grouping features: aquatic stage, reproduction, dispersal, resistance form, food, feeding style, respiration, and locomotion and substratum relation (Appendix S3; Tachet et al. 2002, Schmera et al. 2015). Trait information was unavailable for 28 of the 105 unique taxa identified, mostly among the Diptera, Mollusca, Coleoptera, and Heteroptera. Therefore, we excluded these taxa from analysis of functional diversity, trait richness, and composition analysis. We used a trait database that is fuzzy coded (scores 0–5) according to the affinity of each genus to a particular trait (Tachet et al. 2002). We weighted each trait by multiplying the relative trait affinity scores by the $\log_{10}(x + 1)$ -transformed abundance of each taxon with the trait and dividing this value by the total abundance for each sample, which resulted in a trait \times sample matrix (Dray and Dufour 2007). We used this matrix to calculate functional diversity and trait richness in the R packages *ade4* and *vegan*, respectively (Dray and Dufour 2007, Oksanen et al. 2013). We further tested for changes in trait composition with the trait \times sample matrix by means of Adonis as described previously.

We also selected a priori a group of traits, identified as indicators of flow intermittence and active use of the hyporheic zone as a refuge, to test the effects of drying on trait composition (Bonada et al. 2007, Robertson and Wood 2010). These traits included resistance forms (i.e., eggs, statoblasts, cocoons, diapause, and desiccation resistant cells), small body size (≤ 9 mm), active aerial dispersion, swimmer habit, burrower or interstitial habit, aerial respiration, and asexual reproduction. We used the R package *ade4* (Dray and Dufour 2007) to calculate the proportion of taxa in each sample that had the a priori traits. We then tested for the effects of drying on each $\arcsin\sqrt{x}$ -transformed trait proportion by means of linear mixed-effects models, as described above, where the proportional values for each trait were used as dependent variables and moderate and severe drying classes were analyzed in separate models. We calculated effect sizes and 95% confidence intervals of functional diversity, trait richness, and composition metrics as described above for the taxonomic metrics (Appendix S2).

RESULTS

Quantification of flow intermittence across reaches

The moderate reaches underwent 11 ± 8 (mean \pm SD) drying events, lasting a total of 43 ± 55 d (D_{total}), with $D_{\text{mean}} = 5 \pm 3$ d and $D_{\text{max}} = 17 \pm 4$ d (Table 2). The severe reaches underwent 8 ± 5 drying events, lasting a

total of 104 ± 45 d (D_{total}), with $D_{\text{mean}} = 24 \pm 19$ d and $D_{\text{max}} = 57 \pm 35$ d. Length of time after the final drying event (T_{after}) was 25 ± 5 d at severe reaches and 81 ± 60 d at moderate reaches (Table 2).

Effects of flow intermittence on taxonomic richness and composition of invertebrate communities

A total of 74,143 invertebrates from 105 taxa was collected from the 8 BRs. Mean density of invertebrates was 2513 ± 3356 ind/m² in intermittent and 3635 ± 4921 ind/m² in perennial reaches. No reach type \times sampling period interactive effect was detected when comparing taxonomic richness, density, or the proportion of EPT and OCHD between moderate and severe reaches (Fig. 2A–H, Table 3). Taxonomic richness and density decreased, respectively, over the sampling period by 46 ± 24 and $82 \pm 12\%$ in perennial reaches, 64 ± 20 and $96 \pm 5\%$ in moderate reaches, and 49 ± 27 and $72 \pm 15\%$ in severe reaches (Fig. 2A–D, Table 3). Proportions of EPT and OCHD did not differ among reach types or sampling periods (Fig. 2E–H, Table 3).

Community composition showed no effects of drying events among reaches and sampling periods, regardless of duration (Adonis, reach type \times sampling period interaction, moderate: $p = 0.772$, severe: $p = 0.936$; Fig. 3A, B). Temporal variability in taxonomic composition (i.e., before–after differences) was high (Adonis, sampling period, moderate: $p = 0.003$, severe: $p = 0.005$) and consistent across reach types (Fig. 3A, B).

Effects of flow intermittence on functional diversity, trait richness, and composition of invertebrate communities

Flow intermittence did not affect functional diversity, trait richness, or composition (Fig. 4A–H, Table 4). No interactive effect of sampling period \times reach type was detected when comparing functional diversity and trait richness between moderate and severe reaches (Fig. 4A–D, Table 4). Trait composition among reaches was unaffected by drying events, regardless of drying class (Adonis, moderate: reach type \times sampling period interaction, $p = 0.663$, severe: $p = 0.795$). Furthermore, no interactive effect of reach type \times sampling period was detected on resistance forms (Fig. 4E, F, Table 4), small body size (≤ 9 mm; Fig. 4G, H, Table 4), active aerial dispersion, swimmer habit, burrower or interstitial habit, aerial respiration, or asexual reproduction (data not shown) (linear mixed-effects models, $p > 0.05$).

DISCUSSION

Invertebrate communities in these 8 BRs were highly resilient to flow intermittence, even after severe drying events. Taxonomic richness, composition, and functional

Table 2. Description of moderate and severe drying events across 8 gravel-bed, braided rivers in terms of total number (n , events), total duration (D_{total}), mean duration (D_{mean}), and maximum duration (D_{max}) of drying events, length of time before initial drying event (T_{before}), and length of time after final drying event (T_{after}).

Drying class	River	Reach type	n (events)	D_{total} (d)	D_{mean} (d)	D_{max} (d)	T_{before} (d)	T_{after} (d)
Moderate	Béoux	Intermittent	4	18	4.5	16	52	133
		Perennial			No drying events			
	Buëch	Intermittent	15	125	8.3	23	5	28
		Perennial			No drying events			
	Grand Vallon	Intermittent	20	12	1.4	14	70	30
		Perennial			No drying events			
Jabron	Intermittent	3	15	5.1	14	52	134	
	Perennial			No drying events				
Severe	Duyes	Intermittent	7	72	10.2	34	92	30
		Perennial			No drying events			
	Lez	Intermittent	15	59	9.1	30	25	26
		Perennial			No drying events			
	Roubion	Intermittent	5	132	26.5	105	43	26
		Perennial			No drying events			
	Vançon	Intermittent	3	152	50.7	60	25	19
		Perennial			No drying events			

diversity of communities in intermittent reaches after either moderate or severe drying events were similar to those of perennial reaches in as few as 19 d of flow resumption. These results differ from those of many previous studies in which aquatic communities showed persistent effects of flow intermittence (e.g., del Rosario and Resh 2000, Bogan et al. 2013, Datry et al. 2014a). We attribute these results to: 1) high resilience of invertebrate communities in BRs, whose constituent taxa have been filtered by deterministic process (i.e., niche selection) and may have positive cotolerance to multiple disturbances, and 2) the presence of perennial habitat features, including an expansive hyporheic zone, in which taxa can find refuge during drying events.

Response of invertebrate communities to flow intermittence in BRs

Flow intermittence is considered a primary driver of community structure and composition in rivers (Arscott et al. 2010, Larned et al. 2010, Datry et al. 2014b). In a broad-scale meta-analysis, Datry et al. (2014a) found that taxonomic richness decreased linearly along gradients of flow intermittence, without considering sampling period, in 14 rivers in Europe, North America, and New Zealand. Moreover, strong differences in taxonomic richness and density (see Appendix S2 for effect sizes) generally are found between perennial reaches and reaches experiencing 2–15 mo of channel drying (e.g., del Rosario and Resh

2000, Price et al. 2003, Santos and Stevenson 2011, Bogan et al. 2013). Nevertheless, we found no differences in taxonomic richness and density between intermittent and perennial reaches across these 8 BRs. Furthermore, the mean effect sizes (Hedges' d) in our study were 8× smaller than those found in previous studies (mean = -0.25 ± 0.3 vs -1.96 ± 1.16), where communities in intermittent reaches had lower taxonomic richness and density than perennial reaches, even after 2 mo of flow resumption (Appendix S2). Our results were consistent after both moderate and severe drying events, despite a >3-fold increase in the maximum duration of drying events (mean $D_{\text{max}} = 16$ vs 57 d). Decreases in taxonomic richness and density that occurred over the sampling period were observed across both intermittent and perennial reaches and, therefore, could not be attributed to flow intermittence. Field observations (see Methods) and examination of continuous flow data for the 3 BRs where flow gauging stations were collocated (Buëch, Lez, Roubion) indicated that no high-flow events (i.e., higher than the mean annual discharge) occurred between rewetting and the after-drying sampling period. Rather, such decreases may illustrate the background of seasonal variability in invertebrate richness and density that is common in BRs (Tockner et al. 2010).

Functional diversity and trait composition also can be affected by drying events in freshwater ecosystems (Bonada et al. 2007, Chase 2007). In general, higher proportions of taxa with resistance and resilience traits are found after drying than before and in intermittent vs perennial rivers,

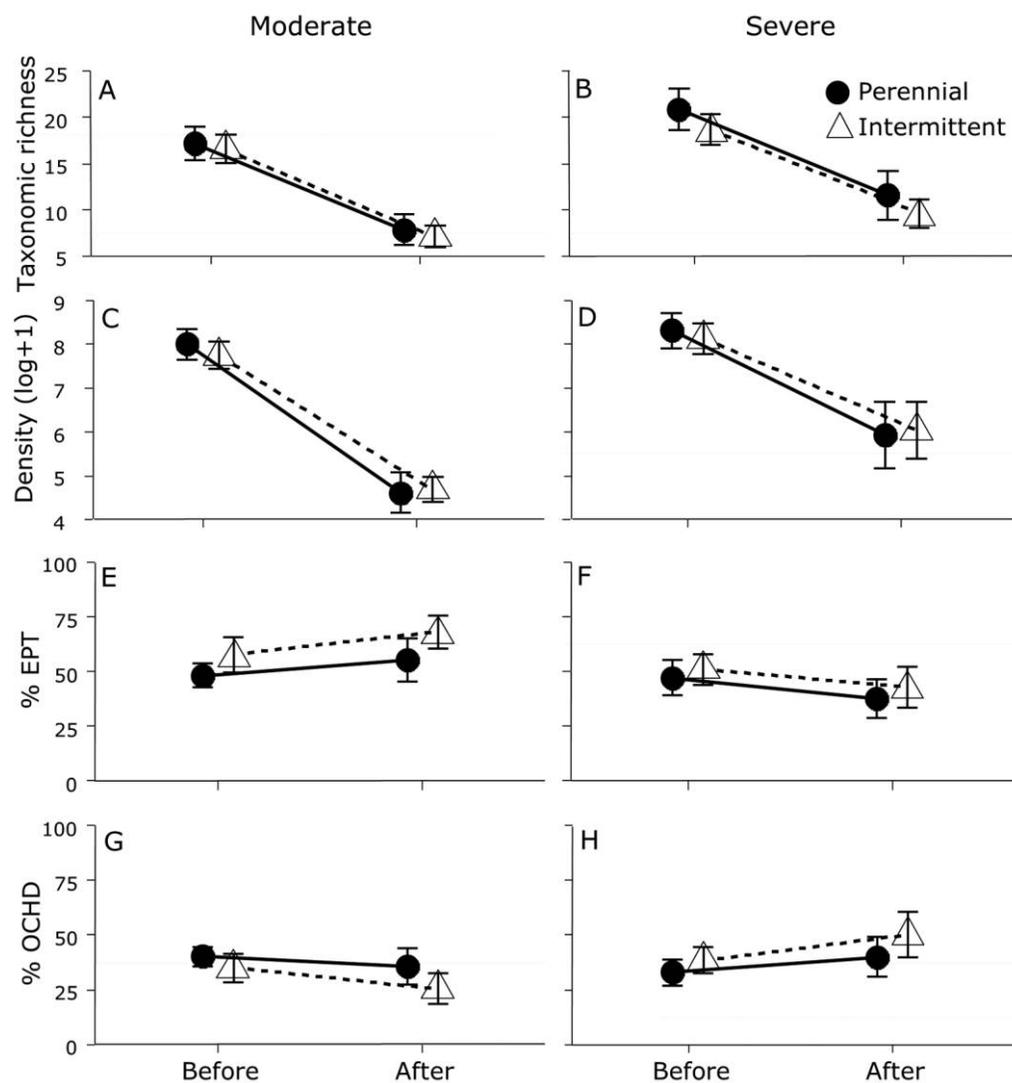


Figure 2. Interaction plots showing change from before to after drying of mean (± 1 SE) taxonomic richness (A, B), $\log_{10}(x + 1)$ -transformed density (individuals/m²) (C, D), % EPT (Ephemeroptera, Plecoptera, Trichoptera) (E, F), and % OCHD (Odonata, Coleoptera, Hemiptera, Diptera) (G, H) in reaches with moderate (A, C, E, G) and severe (B, D, F, H) drying.

indicating that these traits promote the persistence of invertebrate communities in habitats exposed to drying (Bonada et al. 2006, Datry et al. 2014a). The loss of taxa without these traits after drying may lead to decreases in functional diversity. For example, Chase (2007) found that pond drying reduced the diversity of producers (macrophytes and filamentous green algae) because many of these taxa lacked resistance or resilience strategies. In contrast to these studies, we found no decrease in functional diversity or changes in trait composition following drying events, despite a temporal decrease in taxonomic richness. This result indicates that communities in these BRs have functional redundancy, which occurs when different taxa play similar roles in an ecosystem or possess similar traits but

may have different sensitivity to disturbances (Rosenfeld 2002). As in arid-land systems (e.g., Boersma et al. 2014), high functional redundancy in BRs may provide insurance against the loss of ecosystem functions when faced with disturbances.

The resilience of invertebrate communities after drying events is comparatively higher in BRs than other intermittent rivers. In our study, recovery occurred in as few as 19 d following severe drying events. Fowler (2004) found that 95% of pre-drying taxa were present after 7 d of rewetting in 2 braided rivers in New Zealand that dried for 6–14 wk. In contrast, Delucchi (1988) reported that 50% of pre-drying taxa remained lost or had reduced abundances after ≥ 1 mo of rewetting in small–medium

Table 3. Linear mixed-effects models testing the effects of sampling period (before vs after), reach type (perennial vs intermittent), and their interaction on taxonomic richness, $\log_{10}(x + 1)$ -transformed density (individuals/m²), and the $\arcsin\sqrt{x}$ -transformed % EPT (Ephemeroptera, Plecoptera, Trichoptera) and % OCHD (Odonata, Coleoptera, Hemiptera, Diptera).

Drying class	Variable	Source of variation	df	F	p
Moderate	Taxonomic richness	Intercept	80	39.95	<0.0001
		Sampling period	6	82.87	<0.0001
		Reach type	3	0.69	0.4683
		Reach × period	6	1.52	0.2643
	Density	Intercept	80	170.69	<0.0001
		Sampling period	6	158.24	<0.0001
		Reach type	3	2.35	0.2226
		Reach × period	6	1.27	0.3020
	% EPT	Intercept	80	56.46	<0.0001
		Sampling period	6	3.89	0.0961
		Reach type	3	5.76	0.0959
		Reach × period	6	1.10	0.3347
	% OCHD	Intercept	80	34.48	<0.0001
		Sampling period	6	4.16	0.0874
		Reach type	3	3.05	0.1790
		Reach × period	6	0.70	0.4352
Severe	Taxonomic richness	Intercept	80	29.3	<0.0001
		Sampling period	6	18.98	0.0048
		Reach type	3	0.94	0.4035
		Reach × period	6	0.01	0.9546
	Density	Intercept	80	64.01	<0.0001
		Sampling period	6	22.54	0.0032
		Reach type	3	0.01	0.9324
		Reach × period	6	0.09	0.7768
	% EPT	Intercept	80	27.34	<0.0001
		Sampling period	6	3.63	0.1054
		Reach type	3	0.83	0.4304
		Reach × period	6	<0.00	0.9841
	% OCHD	Intercept	80	38.48	<0.0001
		Sampling period	6	0.71	0.4332
		Reach type	3	0.36	0.5890
		Reach × period	6	0.04	0.8468

forested streams that experienced 1–4-mo drying events. Morrison (1990) reported that recovery of taxonomic richness and abundance took ≥ 2 mo after 2–3-mo drying events in 4 small streams in Scotland. Most drastically, drying (2–6 mo) had persistent effects on community composition that lasted 1–2 y (Wood and Armitage 2004, Acuña et al. 2005). Other investigators showed that invertebrate communities also may be more resilient to floods in BRs compared with other rivers (Matthaei et al. 1996). Thus, the effects of flow intermittence on invertebrate communities may vary strongly according to river type,

and further comparisons may help unravel underlying processes that mitigate these effects of drying.

Factors that might promote community resilience and functional redundancy in BRs

High resilience and functional redundancy in BRs may be first explained by a strong filtering (i.e., niche selection) of taxa from the regional species pool with traits allowing them to cope with multiple disturbances (i.e., resistance and resilience; Poff and Ward 1990, Lytle and Poff 2004). When traits enable resistance and resilience

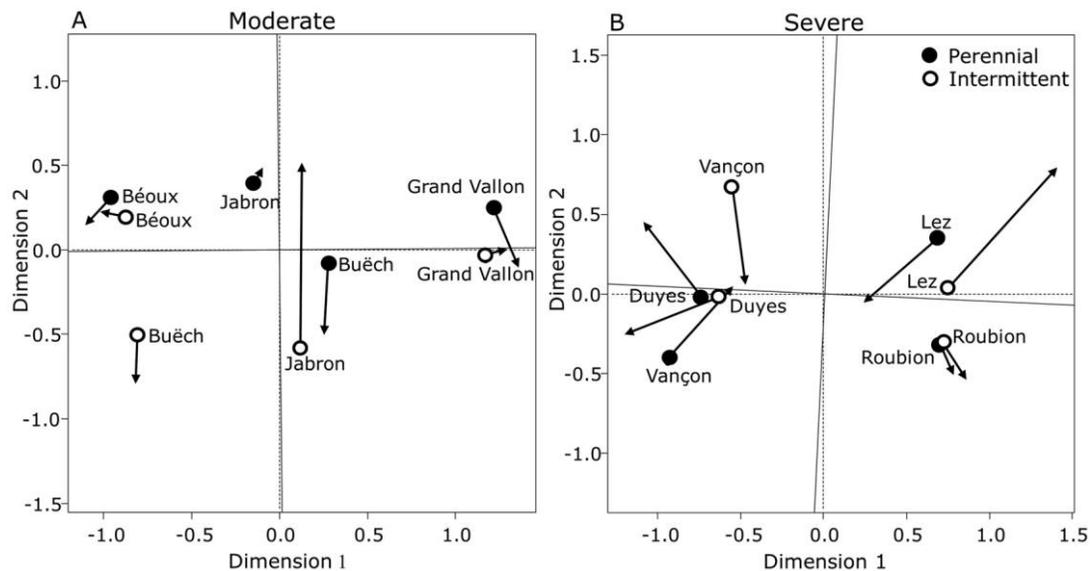


Figure 3. Two-dimensional nonmetric multidimensional scaling (NMDS) plots with Procrustes superimposition based on $\log_{10}(x + 1)$ -transformed density of invertebrates in reaches with moderate (A) and severe (B) drying. Arrows represent the differences in ordinations between the before (origin of the arrows) and after sampling periods (end of the arrows).

of communities to multiple disturbance types, community resilience to a discrete disturbance event is increased (i.e., positive cotolerance; Vinebrooke et al. 2004). For instance, some resilience strategies that allow taxa to disperse to and from refuges during and after floods, including high dispersal ability, inherently promote the recovery of communities after channel drying. Some resistance strategies, such as aerial respiration, allow invertebrates to remain in dry channels until water returns but also help some taxa (e.g., Hemiptera: Belostomatidae) escape flash floods by allowing them to crawl out of the channel to survive in riparian areas (Lytle and Poff 2004). In BRs, the high recurrence rate of disturbances, such as floods and bed scouring, probably eliminates most taxa that are not also resistant or resilient to drying, thereby reducing the effect of a drying event on the community. However, not all traits that promote resistance and resilience are positively correlated across disturbance types (i.e., negative cotolerance; Vinebrooke et al. 2004). For example, taxa with strong flying ability as adults have inherently larger body size in their aquatic stages. Therefore, their ability to fly long distances to colonize previously dried channels hinders them in the aquatic stage where they are more susceptible to floods than are smaller taxa (Townsend and Hildrew 1994). These examples are far from exhaustive but highlight interesting cases of cotolerance in invertebrate taxa to multiple disturbances. Although not often considered by freshwater ecologists, we think that varying responses of freshwater communities to flow intermittence are partially at-

tributable to positive cotolerance with floods and bed scouring.

A fundamental habitat feature of BRs that can promote invertebrate community resilience is the complex patterns of surface-groundwater exchanges, occurring at different scales within the often porous, alluvial river bed (Malard et al. 2003, Capderrey et al. 2013). These exchanges add habitat heterogeneity and offer potential drying refuges for invertebrates (Stanford et al. 2005, Capderrey et al. 2013). Perennial reaches, which are a source of drifting and flying invertebrate colonists, are often maintained by large-scale upwelling zones in BRs (Capderrey et al. 2013). In addition, the gravel river beds in most BRs create an expansive hyporheic zone that can be a refuge for benthic invertebrates during periods of flooding and drying (Boulton et al. 2010). However, evidence remains inconclusive for whether benthic taxa seeking refuge in hyporheic zones actually return to the surface after disturbances (but see Holomuzki and Biggs 2007). This uncertainty is a result, in part, of difficulties in quantifying the number of invertebrates that come from the hyporheic zone compared with from other sources (e.g., drift from upstream, aerial oviposition; Dole-Olivier 2011, Stubbington 2012). Recovery of communities after floods and drying occurs as a function of distance to drying refuges, which affects the colonization rate of drifting and flying invertebrates, with faster recovery corresponding to shorter distances (Fritz and Dodds 2004, Robson et al. 2011). Resilience in BRs probably is high compared with other systems because the pattern of surface-groundwater exchanges across al-

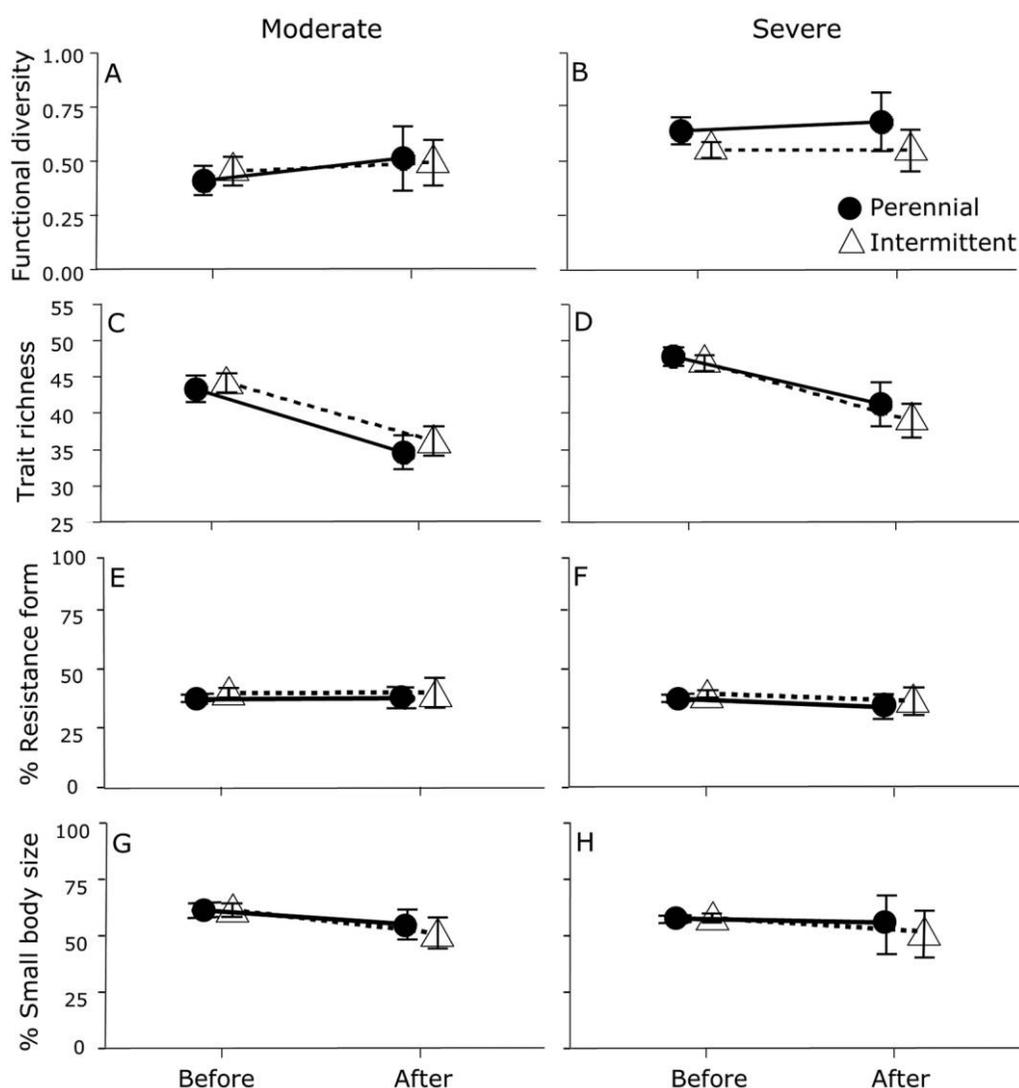


Figure 4. Interaction plots showing change from before to after drying of mean (± 1 SE) functional diversity (A, B), trait richness (C, D), proportion of taxa with resistance form (E, F), and small body size (< 9 mm) (G, H) in reaches with moderate (A, C, E, G) and severe (B, D, F, H) drying.

luvial river beds provides potential sources of colonists that are found either directly below the river bed or within several kilometers (< 10 km) upstream of previously dry channels.

Conclusions

The current understanding of how communities respond to flow intermittence lags behind other facets of freshwater ecology and merits future research emphasis (Larned et al. 2010, Datry et al. 2014b). Our results suggest that the effects of flow intermittence on invertebrate communities may vary strongly according to river type and call for a cross-system comparison to explore parallels and contrasts and to better understand processes that

mitigate the response of communities to drying. As shown in marine systems, such comparisons may reveal that communities in more disturbed systems are also highly resilient because they have a high abundance of disturbance-tolerant taxa (Côté and Darling 2010). In addition, the colonization pathways upon rewetting, and notably the importance of the hyporheic zone to community resilience, deserve more research and, above all, better quantification (Boulton et al. 2010, Dole-Olivier 2011). In the current context of climate change accompanied by increasing flow intermittence and anthropogenic stressors (Larned et al. 2010, Strayer and Dudgeon 2010), understanding and quantifying processes that contribute to ecosystem resilience are essential. Future research in naturally highly disturbed systems, such as BRs, could help to advance this

Table 4. Linear mixed-effects models testing the effects of sampling period (before vs after), reach type (perennial vs intermittent), and their interaction on the arcsin \sqrt{x} -transformed proportion of taxa with resistance forms and small body size (≤ 9 mm), functional diversity, and trait richness.

Drying class	Variable	Source of variation	df	F	p	
Moderate	% Resistance form	Intercept	80	495.68	<0.0001	
		Sampling period	6	0.27	0.6192	
		Reach type	3	0.40	0.5704	
		Reach \times period	6	0.04	0.8412	
		% Small body size	Intercept	80	300.39	<0.0001
			Sampling period	6	4.45	0.0795
	Reach type		3	0.42	0.5650	
	Reach \times period		6	0.33	0.5857	
	Functional diversity	Intercept	79	27.56	<0.0001	
		Sampling period	6	0.37	0.5630	
		Reach type	3	0.85	0.4253	
		Reach \times Period	6	1.76	0.2326	
	Trait richness	Intercept	79	298.13	<0.0001	
		Sampling period	6	100.25	0.0001	
		Reach type	3	0.09	0.7885	
		Reach \times Period	6	3.60	0.1067	
	Severe	% Resistance form	Intercept	80	423.50	<0.0001
			Sampling period	6	1.77	0.2315
Reach type			3	0.11	0.7606	
Reach \times Period			6	<0.01	0.9485	
% Small body size			Intercept	80	458.90	<0.0001
			Sampling period	6	0.15	0.7078
		Reach type	3	0.08	0.7942	
		Reach \times period	6	0.12	0.7408	
Functional diversity		Intercept	79	49.76	<0.0001	
		Sampling period	6	0.03	0.8719	
		Reach type	3	2.13	0.2406	
		Reach \times period	6	0.12	0.7367	
Trait richness		Intercept	79	327.17	<0.0001	
		Sampling period	6	10.24	0.0186	
		Reach type	3	0.51	0.5273	
		Reach \times period	6	0.12	0.7455	

understanding and improve the ability to predict the responses of communities to future environmental changes.

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