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Do lentic and lotic communities respond similarly to drying?

VÉRONIQUE ROSSET,^{1,†} ALBERT RUHI,² MICHAEL T. BOGAN,³ AND THIBAUT DATRY¹

¹*Irstea Lyon, UR MALY, 5 rue de la Doua, 69100 Villeurbanne, France*

²*National Socio-Environmental Synthesis Center (SESYNC), University of Maryland, Annapolis, Maryland 21401 USA*

³*School of Natural Resources and the Environment, University of Arizona, 1064 E. Lowell Street, Tucson, Arizona 85716 USA*

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Abstract. Disturbance is a central factor shaping composition, structure, and dynamics of local communities. Drying is a disturbance that occurs in aquatic ecosystems globally and can strongly influence their communities. Although the effects of drying may depend on ecosystem connectivity and the dispersal abilities of resident species, there have been no comparisons of community responses to drying between lentic and lotic ecosystems across different climates. Here, we predicted that drying would have stronger effects on aquatic communities in isolated lentic ecosystems than in dendritic lotic ecosystems, owing to the higher hydrological connectivity of the latter, and that drying would have stronger effects on passive than on active dispersers, because of the potentially higher recolonizing ability of the latter. We tested these predictions by comparing alpha diversity, phylogenetic relatedness, and beta diversity for active and passive dispersers, in both ecosystem types across five climatic regions. Drying caused greater declines in alpha diversity in lentic than in lotic ecosystems. Communities that experienced drying were more similar to one another than those of perennial sites, and this pattern was especially pronounced in lentic ecosystems. In contrast, drying did not influence the contributions of turnover and richness gradients to beta diversity. Additionally, dispersal mode did not influence community responses to drying. Relatively weaker effects of drying in lotic compared to lentic systems were likely due to the hydrological connectivity among perennial and temporary river sites, which may facilitate dispersal of organisms to escape drying and recolonize rewetted sites. Collectively, our results suggest that habitat connectivity may ameliorate (and fragmentation may worsen) the impacts of drying disturbance. This is an important finding in light of increasing drying and concomitant aquatic habitat fragmentation under global change.

Key words: alpha diversity; beta diversity; connectivity; disturbance; flow intermittence; hydroperiod; macroinvertebrates; phylogenetic relatedness; ponds; streams; wetlands.

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† **E-mail:** veronique@rosset.org

INTRODUCTION

Disturbance is a central concept in ecology and is widely recognized to influence populations, communities, and ecosystems (Sousa 1984, Hobbs and Huenneke 1992). Frequent or intense disturbance shapes community composition by filtering out sensitive species (Poff 1997, Verdu and Pausas 2007), influencing richness (e.g., Connell 1979, Townsend et al. 1997). Drying, defined as the complete disappearance of surface water,

represents a major disturbance for aquatic organisms as recognized by most ecologists (e.g., Williams 2006, Greig et al. 2013, Leigh and Datry 2016). Drying has been identified as a primary driver of community structure in marine intertidal zones (Dayton 1971), freshwater lentic (Williams 2006), and lotic ecosystems (Boulton 2003).

Lentic and lotic ecosystems differ fundamentally in local habitat conditions (e.g., presence or absence of flow, water residence time) and also in physical connectivity. Lentic ecosystems are

discrete aquatic habitats in a terrestrial matrix (De Meester et al. 2002), while lotic ecosystems are generally continuous habitats linked by unidirectional flow within dendritic river networks (Fagan 2002). Habitat geometry, that is, the amount, shape, fragmentation, and connectivity of habitats, can influence community structure (France and Duffy 2006, Starzomski and Srivastava 2007), and hydrological connectivity can greatly facilitate dispersal of aquatic taxa and their coexistence in multiple sites (Bilton et al. 2001). Consequently, drying could have different effects on communities of temporary and perennial lentic and lotic ecosystems. While aerial dispersal is the main resilience strategy by which lentic macroinvertebrates can actively escape a drying habitat, lotic taxa can track receding flow upstream, or drift downstream, in search of perennial habitat (Bilton et al. 2001). Upon rewetting, recolonization may occur more easily in lotic than in lentic ecosystems due to this higher connectivity. Similarly, community responses to drying may depend on how different dispersal modes are represented in a local community. In fragmented habitats, taxa with flying adult stages can actively disperse overland in search of new habitat (e.g., winged insects; hereafter *active dispersers*); in contrast, flightless taxa rely on passive transport via the elements or other organisms (e.g., snails transported by birds; hereafter *passive dispersers*).

Drying can alter multiple facets of community structure, including the number of taxa at a given site (*alpha diversity*), their phylogenetic relatedness, and the temporal and/or spatial dissimilarity in community composition between sites (*beta diversity*). Beyond moderate levels of disturbance (sensu Connell 1979), alpha diversity at a given habitat site generally increases with increasing water permanence (e.g., Wissinger et al. 2009, Arscott et al. 2010, Datry et al. 2014, Brendonck et al. 2015). The relatively high habitat connectivity of lotic ecosystems may lead to “rescue effects” (immigrants recolonizing and saving a population from local extirpation) being observed more often in streams (Brown and Kodric-Brown 1977). This should maintain high levels of alpha diversity even in streams that dry frequently or for extended periods. Similarly, a high prevalence of active dispersers in a community may maintain alpha diversity via source–sink metacommunity dynamics (Wissinger 1997, Leibold et al. 2004).

Drying does not extirpate random members of a local community, but it does exclude taxa that lack the ability to recolonize after, or persist during, dry periods. Thus, the degree of phylogenetic relatedness among taxa within a local community may be shaped by drying (Ruhi et al. 2013a). In particular, traits conferring resistance to drying (i.e., ability to withstand desiccation in situ) and resilience to drying (i.e., ability to recolonize following rewetting) are often shared within phylogenetic groups (e.g., desiccation-resistant eggs of branchiopods). Thus, unevenness in phylogenetic trees may decrease with increasing water permanence, and this relationship may be attenuated by habitat connectivity. Phylogenetic relatedness may respond to various environmental filters from water availability to fire frequency (Warwick and Clarke 1998, Heino et al. 2007, Cavender-Bares et al. 2009) and, as such, drying should increase similarity among members of local communities.

Finally, drying can also influence beta diversity. Evidence from lentic ecosystems indicates that the lack of permanent water may filter sensitive taxa from the regional taxonomic pool, leading to a specific subset of disturbance-adapted taxa dominating at temporary sites (Poff 1997, Chase 2007, Ruhi et al. 2013b). This filtering of taxa leads to differences in beta diversity and its components, namely turnover (i.e., taxa replacements) and richness (i.e., taxa additions and deletions, often called nestedness). As with alpha diversity, the effects of water permanence on beta diversity can be mediated by habitat connectivity and taxa dispersal modes. Low dispersal or connectivity may result either in low beta diversity, when a few good dispersers predominate in isolated sites, or in high beta diversity, when stochastic colonization prevails (De Meester et al. 2002, Vanschoenwinkel et al. 2013). High dispersal or connectivity may result in reduced beta diversity due to dispersal-driven homogenization (Mouquet and Loreau 2003). This dispersal homogenization can lead to larger contributions of richness gradients (nestedness) to observed beta diversity values, whereas colonization and priority effects may result in taxa turnover being the primary driver of beta diversity.

In the present study, we analyzed community responses to drying in small lentic waterbodies (ponds) and rivers from North America and

Europe, comparing taxa dispersal modes and communities from different climatic regions. We selected macroinvertebrates as a focal group because they occur in a wide range of climatic and environmental conditions (Rosenberg and Resh 1993) and possess contrasting dispersal modes (Bilton et al. 2001). Published and new data were combined to address this overarching question and test the generality of five predictions across climates. First, alpha diversity should increase with water permanence, with stronger effects of drying in lentic than in lotic ecosystems (Fig. 1A, *prediction 1*). Second, drying should select for groups of taxa with traits conferring resistance or resilience to this disturbance, increasing phylogenetic relatedness of communities in temporary sites, especially in lentic ecosystems (Fig. 1B, *prediction 2*). Third, given the higher isolation of lentic ecosystems, lentic sites should share lower proportions of taxa than lotic sites, leading to turnover gradients in lentic ecosystems and to richness gradients (i.e., communities in temporary sites being subsets of perennial ones) in lotic ecosystems (Fig. 1C, *prediction 3*). Fourth, the high taxonomic richness expected in perennial habitats should lead to high local contributions to beta diversity in both lotic and lentic ecosystems, but, owing to the prevalence of temporary pond specialists, turnover gradients in addition to richness gradients should be important in temporary lentic habitats (Fig. 1D, *prediction 4*). Finally, all these patterns (predictions 1–4) should be more pronounced in passive dispersers than in active dispersers, as the higher recolonization abilities of the latter could dampen their responses to drying (Fig. 1, *prediction 5*).

METHODS

Identification of data for inclusion

We gathered data from published and unpublished studies of ponds and rivers from Europe and North America on macroinvertebrate composition including both temporary (drying) and perennial (non-drying) sites. For this purpose, any system that dried for any duration in a typical year was considered as temporary (Williams 2006). To locate published data sources, we searched an online database (ISI Web of Science) and a search engine (Google Scholar) using the terms: *temporary* OR *ephemeral* OR *intermittent**

combined with either *freshwater** OR *streams* OR *stream* OR *rivers* OR *river* OR *ponds* OR *pond* OR *wetland** OR *pools* OR *pool*. As drying occurs in all biomes and responses to drying may change with climate harshness (Ruhi et al. 2013a), we covered the five climatic groups of the Köppen-Geiger classification: *Arid Bsk*, *Mediterranean Cs*, *Temperate Cf*, *Cold D*, and *Polar ET*. This selection process resulted in a 2×2 design with two ecosystem types (ponds and rivers) and two disturbance regimes (temporary and perennial) for one climate group. Due to the scarcity of perennial sites in arid climates, only temporary sites were available for ponds under this climate.

Each selected study included multiple sites within each climatic group, which we treated as replicates or “local communities.” Sites were only included if (1) they were natural (i.e., not man-made or restored), unimpaired ecosystems; (2) data were reported separately for each site; (3) data were available for the whole macroinvertebrate community and sampling methods adequately targeted all groups; (4) qualitative data were available about the water permanence of the sites; (5) taxa were identified at the genus level or lower for all groups with sufficient taxonomic knowledge; and (6) enough time had elapsed before sampling to allow for colonists to arrive and a diverse community to be present (e.g., generally >60 d; Bogan et al. 2015). We detected no significant effects of the different methodologies, different taxonomic resolutions, and different sampling efforts on taxonomic richness or composition (Appendix S1). Similarly, taxa accumulation curves revealed sufficient sampling effort (Appendix S1). This selection procedure provided 116 sites (65 ponds and 51 river sites), ranging from 4 to 18 sites per climate group for river ecosystems and from 8 to 18 for pond ecosystems (see Table 1). Descriptions and references of the selected studies are given in Appendix S2.

Data analysis

Differences in alpha diversity.—Alpha diversity was defined here as the observed taxonomic richness of a local community (see sampling effort tests via taxa accumulation curves in Appendix S1). To test whether higher alpha diversity occurred in perennial compared with temporary habitats, independently or not of ecosystem

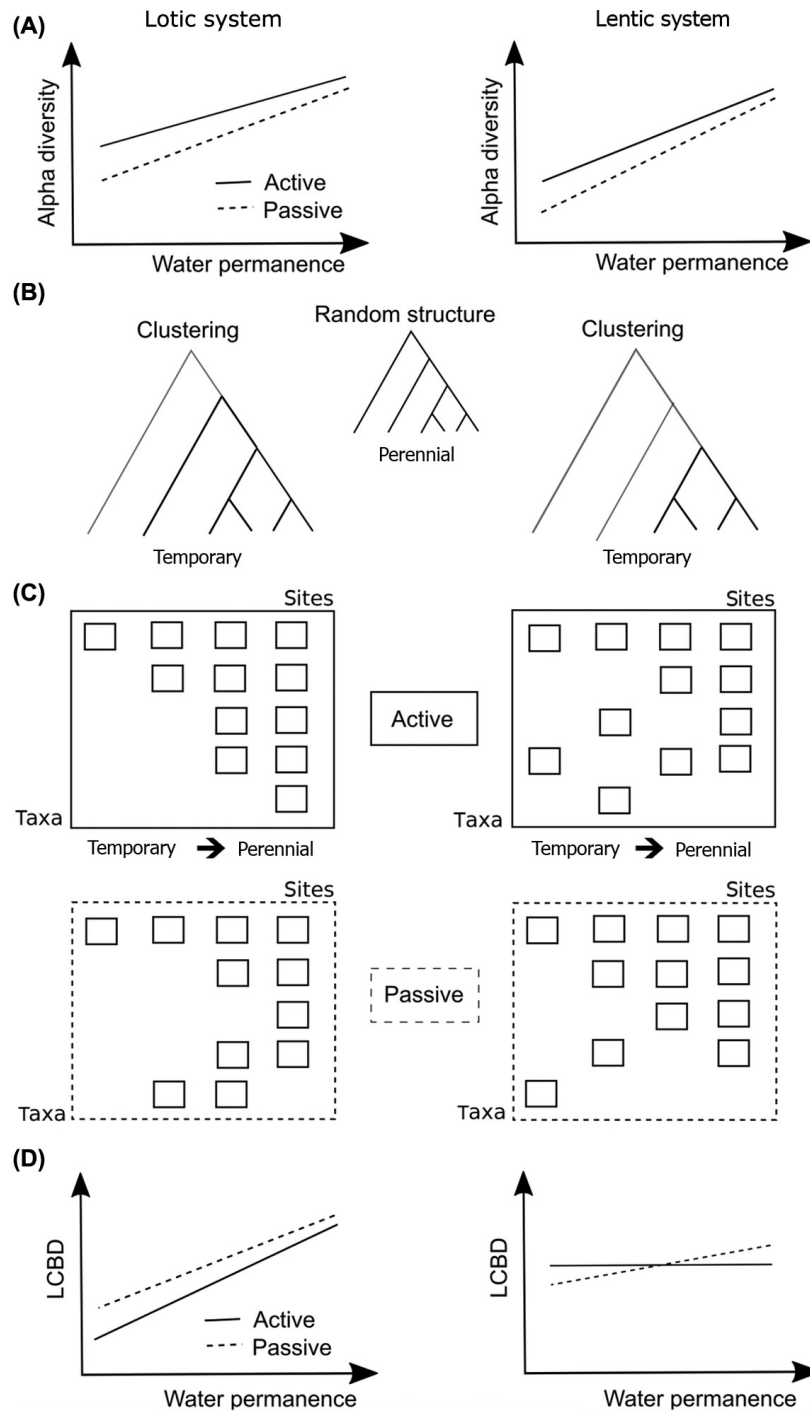


Fig. 1. Conceptual representations of community responses to drying disturbance for active dispersers (solid line) and passive dispersers (dashed line) in lentic and lotic ecosystems. (A) Predicted alpha diversity patterns. (B) Predicted phylogenetic relatedness for all taxa represented by phylogenetic trees where species are at the base and gray lines represent species loss. (C) Predicted turnover and richness gradients to beta diversity represented by packed matrices of species \times sites. (D) Predicted patterns of local contributions to beta diversity (LCBD).

type (*prediction 1*), we used generalized linear mixed-effects models with Gaussian error distributions (lme4 package; R Development Core Team 2008). Mixed-effects models allowed us to incorporate both fixed and random effects and to test nested models (Zuur et al. 2009). Models were run with the original raw data, but models with other taxonomic resolutions are available in Appendix S5.

Four nested mixed-effects models that progressively decreased in complexity were tested, with alpha diversity as a dependent variable: (1) a model with a fixed effect of interaction between drying and ecosystem type which tested whether the effect of drying varied between ecosystems; (2) a model with a fixed effect of drying and ecosystem type without interaction which tested whether the effect of drying varied between ecosystems independently; (3) a model with a fixed effect of drying across both ecosystem types which tested a similar effect of drying in

both ecosystems; and (4) a null model with a random intercept which tested random differences between sites. Site was a random effect in each model, which in turn controlled for variation in sampling methods across studies. The statistical significance levels for the fixed and random effects in the best-fitting models were determined using likelihood-ratio tests on models with and without each effect (Bolker et al. 2009). To select the most parsimonious models, we used the minimum Akaike's information criterion (AIC).

To compare the magnitude of drying effects on alpha diversity between temporary and perennial sites, we computed Cohen's d (or standardized differences), defined as the difference between the means divided by the root mean square of two standard deviations (Cohen 1988). Larger d values mean higher effect sizes, and positive d values reflect higher values in perennial than in temporary sites.

Table 1. Geographic, climatic, and methodological details of the studies included in the paper.

Location	Site	System	Climate	No. sites	Method	No. samples/site	No. visits/site	Spatial scale	Authors†
Grand Casablanca, Morocco	Casablanca	Ponds	Arid	6	Modified Hess sampler	>25	26	10 km ²	Metge (1986)
Arizona, USA	Garden and Huachuca	Rivers	Arid	9	D-net	3–9	1–3	24 km	Bogan et al. (2013)
Latium, Italy	Romane Coastal Reserve	Ponds	Med.	15	Hand-net	5–17	1	100 km ²	Della Bella et al. (2005), Della Bella (2005)
Provence, France	Asse	Rivers	Med.	13	Hess sampler	10	5	20 km	Datry et al. (2014)
Oxfordshire, UK	Oxfordshire	Ponds	Temp.	8	Hand-net	9–24	3	90 km ²	Pond Action (1994)
Rhône-Alpes, France	Albarine	Rivers	Temp.	18	Hess sampler	10	5	30 km	Datry (2012)
Colorado, USA	Mexican Cut Nature Preserve	Ponds	Cold	18‡	D-net and drop box	>25	>8	15 km ²	Wissinger et al. (1999)
Indiana, USA	Sycamore	Rivers	Cold	8	Modified Hess sampler	16	4	5 km	Unpublished data§
Grisons, Switzerland	Macun National Park	Ponds	Polar	18	Hand-net	2–19	1	2 km ²	Oertli et al. (2008)
Grisons, Switzerland	Macun National Park	Rivers	Polar	6	Kick net	7	7	2 km	Ruegg et al. (2004)

Note: Med., Mediterranean; Temp., Temperate.

† See Appendix S2 for complete references.

‡ 41 samples were taken in the original study, but a random subsample of 18 sites was used (see Appendix S1).

§ Data obtained from Ken Fritz, US EPA, USA.

Differences in phylogenetic relatedness.—To test whether relatedness was higher in temporary than in perennial ecosystems (*prediction 2*), we generated a taxonomic distance matrix for each study, with distance values representing lengths of paths connecting taxa pairs, traced across a standard taxonomic (or Linnean) tree that considered six taxonomic levels, from species to phylum (after Clarke and Warwick 1998). Taxonomy was used as a proxy for phylogeny because the use of taxonomic categories only slightly affects the estimation of variation in phylogenetic structures (Hardy and Senterre 2007). In particular, we computed average taxonomic distinctness (hereafter “Delta+”), a measure of how distantly related species are, on average, within a community. Since average pairwise distances may be influenced by the number of species present in a given tree, a null model allowed us to test whether the observed Delta+ was higher or lower than predicted by taxonomic richness. To this end, we used the TAXDTEST routine (Clarke et al. 2008) to obtain a null expectation of Delta+ values by drawing random subsets of species from the regional pool (after 999 permutations). Subsequently, observed and expected Delta+ values were compared, and samples (i.e., communities) falling outside the interval obtained with the 95% of the simulated values were considered to have higher- or lower-than-expected relatedness. Lower-than-expected Delta+ values reflect taxonomic clustering, whereas higher-than-expected values reflect overdispersion. The significance of the sample statistic (hereafter %Delta+) is thus a measure of non-randomness in the phylogenetic structure (after Clarke and Warwick 1998). Both Delta+ and %Delta+ were used as dependent variables in the same four linear mixed models computed for alpha diversity. Cohen’s *d* was again computed to compare the magnitude of drying effects between perennial and temporary sites.

Differences in beta diversity.—To test whether beta diversity was dominated by turnover gradients in ponds and by richness gradients in streams (*prediction 3*), beta diversity was partitioned into its overall turnover and richness components using Legendre (2014) formulae, and “local contributions to beta diversity”, *LCBD*, were computed for each site. Local contributions to beta diversity (*LCBD*) indicate to what extent a site differs in composition from a virtual “mean site” and can

be due to a particular community (1) having a low/high number of taxa relative to other communities or (2) having the same number of taxa but different identities (e.g., some singletons). Since these mechanisms are not antithetical, beta diversity can also emerge as (3) a combination of richness and taxa identity gradients.

Overall beta diversities and *LCBD* were calculated on matrices that combined temporary and perennial sites for each climate and ecosystem type. Beta diversity was calculated with Sørensen and Jaccard indices from both Podani and Baselga families (Legendre 2014). The four indices were highly correlated (mean Pearson’s correlation coefficient of 0.92), and the Podani-family Jaccard index was used thereafter (Legendre 2014). To test whether higher *LCBD* occurred in perennial compared with temporary sites (*prediction 4*), *LCBD* values were used as a dependent variable in four linear mixed models as described previously for alpha diversity and phylogenetic relatedness. Models were run with the original raw data, but models with other taxonomic resolutions are available in Appendix S5.

Differences between dispersal modes.—To test whether differences in responses to drying were related to dispersal mode (*prediction 5*), we classified taxa as *active* or as *passive dispersers* (see assignments in Appendix S3). Active dispersers are capable of flying (i.e., adult aquatic insects), while passive dispersers may actively disperse through water but only passively overland (e.g., crustaceans). Differences in alpha and beta diversity responses to drying were investigated for these two dispersal categories. Differences in phylogenetic relatedness responses to drying were investigated for the whole community, because dispersal mode likely has a phylogenetic signal that would interfere with the expected responses.

RESULTS

Differences in alpha diversity

Supporting *prediction 1*. Alpha diversity was better explained by the interaction between drying and ecosystem type (i.e., pond compared with river, first model, Table 2) than by their individual effects or by a random effect. Alpha diversity was higher at perennial than at temporary sites, and this pattern was similar in pond and river ecosystems (Fig. 2). However, the effect

size of drying on alpha diversity was higher or similar in ponds compared to rivers (Cohen's $d = 0.66$ and 0.73 for active and passive dispersers, respectively) than in rivers (Cohen's $d = 0.75$ and 0.32 , respectively). Alpha diversity patterns were consistent across climatic groups, despite differences in effect size (75% of the studies for ponds and 63% for rivers; Appendix S4).

Differences in phylogenetic relatedness

Supporting prediction 2. Phylogenetic relatedness was explained by the interaction between drying and ecosystem type rather than by their

individual effects or by a random effect (first model, Table 3). In ponds, average taxonomic distinctness (Delta+) was lower in temporary than in perennial sites (Cohen's $d = 0.71$), meaning that communities of temporary sites were more clustered than those of perennial ones (Fig. 3). Observed differences between perennial and temporary habitats were smaller in rivers (Cohen's $d = -0.46$), and there was no stronger clustering in temporary rivers relative to perennial ones (Fig. 3). Differences in the probability of random structure (%Delta+) between perennial and temporary habitats were smaller for both ponds and rivers (Cohen's $d = -0.16$ and

Table 2. AIC, likelihood ratios, and P -values of the likelihood-ratio tests for the four different nested models for alpha diversity and local contributions to beta diversity (LCBD) of macroinvertebrates with active or passive dispersal mode (see *Methods* for details).

Metric	Model number	Model terms	AIC	logLik	Test	P -value
Alpha diversity Active dispersers	1	Drying × ecosystem	807.10	-394.55	None	NA
	2	Drying + ecosystem	810.09	-397.04	1 vs. 2	0.0255
	3	Drying	813.87	-399.94	1 vs. 3	0.0046
	4	Random	822.69	-405.35	1 vs. 4	0.0001
LCBD total Active dispersers	1	Drying × ecosystem	-441.12	229.56	None	NA
	2	Drying + ecosystem	-448.86	232.43	1 vs. 2	0.0166
	3	Drying	-389.90	201.95	1 vs. 3	0.0000
	4	Random	-396.96	204.48	1 vs. 4	0.0000
LCBD richness Active dispersers	1	Drying × ecosystem	-270.10	144.05	None	NA
	2	Drying + ecosystem	-276.71	146.35	1 vs. 2	0.0319
	3	Drying	-273.39	143.69	1 vs. 3	0.6999
	4	Random	-280.92	146.46	1 vs. 4	0.1857
LCBD turnover Active dispersers	1	Drying × ecosystem	-239.80	128.90	None	NA
	2	Drying + ecosystem	-245.43	130.71	1 vs. 2	0.0568
	3	Drying	-241.68	127.84	1 vs. 3	0.3466
	4	Random	-247.16	129.58	1 vs. 4	0.7150
Alpha diversity Passive dispersers	1	Drying × ecosystem	591.58	-286.79	None	NA
	2	Drying + ecosystem	595.36	-289.68	1 vs. 2	0.0162
	3	Drying	595.24	-290.62	1 vs. 3	0.0217
	4	Random	601.17	-294.59	1 vs. 4	0.0014
LCBD total Passive dispersers	1	Drying × ecosystem	-414.47	216.23	None	NA
	2	Drying + ecosystem	-422.67	219.34	1 vs. 2	0.0128
	3	Drying	-386.68	200.34	1 vs. 3	0.0000
	4	Random	-396.63	204.32	1 vs. 4	0.0000
LCBD richness Passive dispersers	1	Drying × ecosystem	-252.42	135.21	None	NA
	2	Drying + ecosystem	-259.30	137.65	1 vs. 2	0.0272
	3	Drying	-259.80	136.90	1 vs. 3	0.1850
	4	Random	-268.62	140.31	1 vs. 4	0.0169
LCBD turnover Passive dispersers	1	Drying × ecosystem	-118.26	68.13	None	NA
	2	Drying + ecosystem	-124.47	70.24	1 vs. 2	0.0401
	3	Drying	-131.22	72.61	1 vs. 3	0.0113
	4	Random	-138.84	75.42	1 vs. 4	0.0022

Note: Significant P -values (<0.05) are in bold.

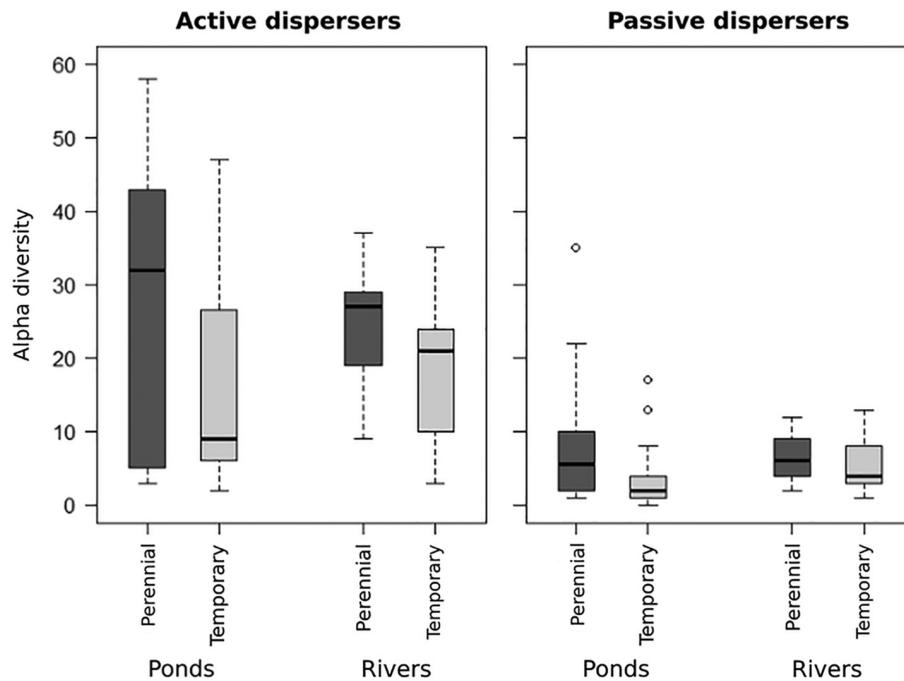


Fig. 2. Alpha diversity of macroinvertebrates with active and passive dispersal modes in perennial and temporary river and pond ecosystems. Vertical boxes represent the interquartile range (Q3–Q1), within which the line represents the median. Whiskers represent the largest non-outlier values, and dots represent outlier values.

0.26, respectively) and the structure of most sites did not differ from a random structure, with observed Delta+ falling within the expected range in 90% of the sites. Phylogenetic relatedness patterns were consistent across climates, but effect sizes differed by climate (Appendix S4).

Differences in beta diversity

In contrast with prediction 3, the relative contribution of richness and turnover gradients to

overall beta diversity did not differ between ecosystem types (Fig. 4), and active and passive dispersers contributed similarly to these patterns. An equilibrium between richness and turnover gradients was observed in 60% of the datasets for ponds and in 80% of the datasets for rivers (Appendix S4).

Contrary to prediction 4, LCBD for total dissimilarity were best explained by drying alone (third model, Table 2); that is, LCBD for total

Table 3. AIC, likelihood ratios, and P-values of the likelihood-ratio tests for the four different nested models for average taxonomic distinctness (Delta+) and probability of a random structure (%Delta+; see Methods for details).

Metric	Model number	Model terms	AIC	logLik	Test	P-value
Delta+	1	Drying × ecosystem	696.78	−339.39	None	NA
	2	Drying + ecosystem	706.40	−345.20	1 vs. 2	0.0007
	3	Drying	708.24	−347.12	1 vs. 3	0.0004
	4	Random	708.08	−348.04	1 vs. 4	0.0006
%Delta+	1	Drying × ecosystem	1104.51	−543.26	None	NA
	2	Drying + ecosystem	1111.12	−547.56	1 vs. 2	0.0033
	3	Drying	1114.85	−550.43	1 vs. 3	0.0008
	4	Random	1118.46	−553.23	1 vs. 4	0.0002

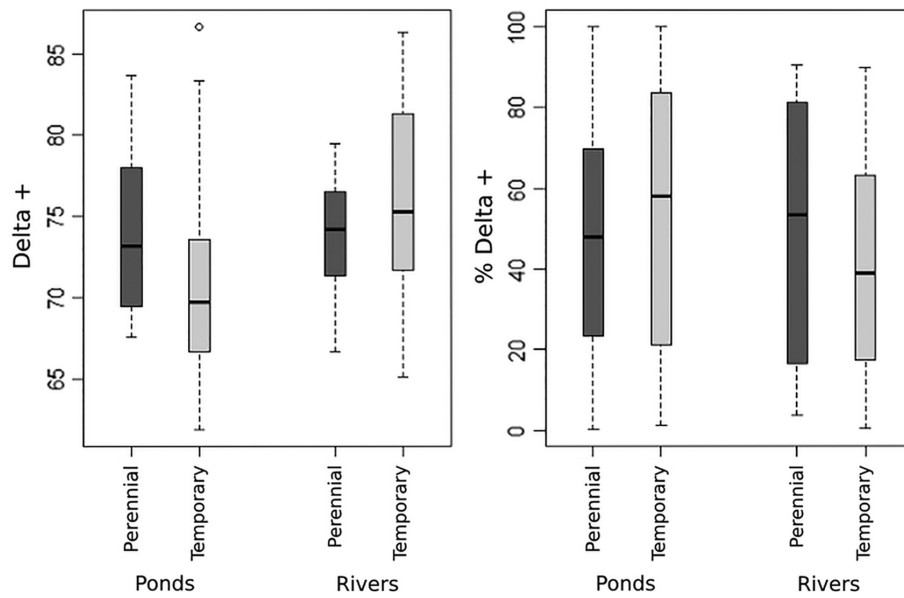


Fig. 3. Average taxonomic distinctness, Delta+, and probabilities of a random phylogenetic structure, %Delta+, in perennial and temporary river and pond ecosystems. Graphical representation as in Fig. 2.

dissimilarity differed between temporary and perennial sites, but independently of ecosystem type (ponds compared with rivers). In contrast to total dissimilarity, but similar to *prediction 4*, LCBD for turnover and richness dissimilarities were explained by the interaction between drying and ecosystem type (first model, Table 2). Differences in LCBD (total, turnover, and richness) were very

small for both active and passive dispersers (mean Cohen's $d = 0.17$, Fig. 5). In contrast to *prediction 4*, larger differences between perennial and temporary habitats were not observed in rivers relative to ponds (mean Cohen's $d = 0.18$ and 0.16 , respectively). This pattern was consistent across climates, despite differences in effect size (75% of the datasets for ponds and 60% for rivers; Appendix S4).

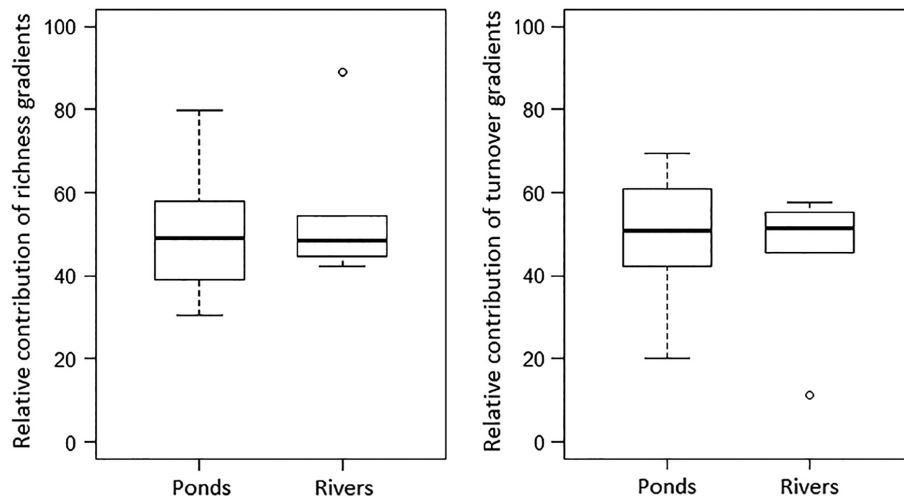


Fig. 4. Relative contribution of richness gradients (left) and turnover gradients (right) to overall beta diversity in perennial and temporary river and pond ecosystems. Graphical representation as in Fig. 2.

DISCUSSION

Community responses to drying were quantified in freshwater ecosystems across a range of climates. Assessing variation in richness, relatedness, and beta diversity showed that overall, drying had more pronounced effects on communities of isolated, lentic habitats, than those of connected, lotic ecosystems. Although our study focused on the abiotic filter of drying on community structure and diversity, biotic interactions may also contribute to the observed patterns (Wellborn et al. 1996, McHugh et al. 2014). Collectively, our findings suggest that hydrological connectivity mediates community responses to drying disturbance. This highlights the multiple scales at which disturbance may occur, and the interactions among these scales. Drying, in particular, has a twofold effect by locally controlling habitat and regionally controlling connectivity.

Differing responses to drying disturbance between lentic and lotic ecosystems

Alpha diversity.—Water permanence was associated with high alpha diversity, in particular in lentic ecosystems. Interactive effects of landscape

structure and disturbance have been observed for alpha richness of macroinvertebrates in rock pools (Vanschoenwinkel et al. 2013), for protozoa and rotifers in aquatic microcosms (Altermatt et al. 2011), and for microarthropods in terrestrial moss patches (Starzomski and Srivastava 2007). Despite some perennial sites being larger than temporary sites in the present study, the observed reduction in alpha diversity with decreasing water permanence is likely due to environmental filtering of sensitive taxa by drying disturbance. Recovery from drying relies on resistance and resilience mechanisms (e.g., Bogan et al. 2015). If resistance strategies are prevalent in both lentic and lotic ecosystems (Wellborn et al. 1996, Bèche and Statzner 2009), then the reduced effect of drying observed in lotic ecosystems is likely due to differences in resilience between lotic and lentic communities. The higher connectivity of lotic ecosystems may increase the ability of taxa to escape drying sites and recolonize rewetted sites via aquatic dispersal (e.g., drift and upstream migration; Bilton et al. 2001). In contrast, aerial colonization (active or passive through zoochory) is the primary means of recolonizing rewetted lentic habitats (e.g., De Meester et al. 2002) and may be more stochastic (Ruhi et al. 2013b).

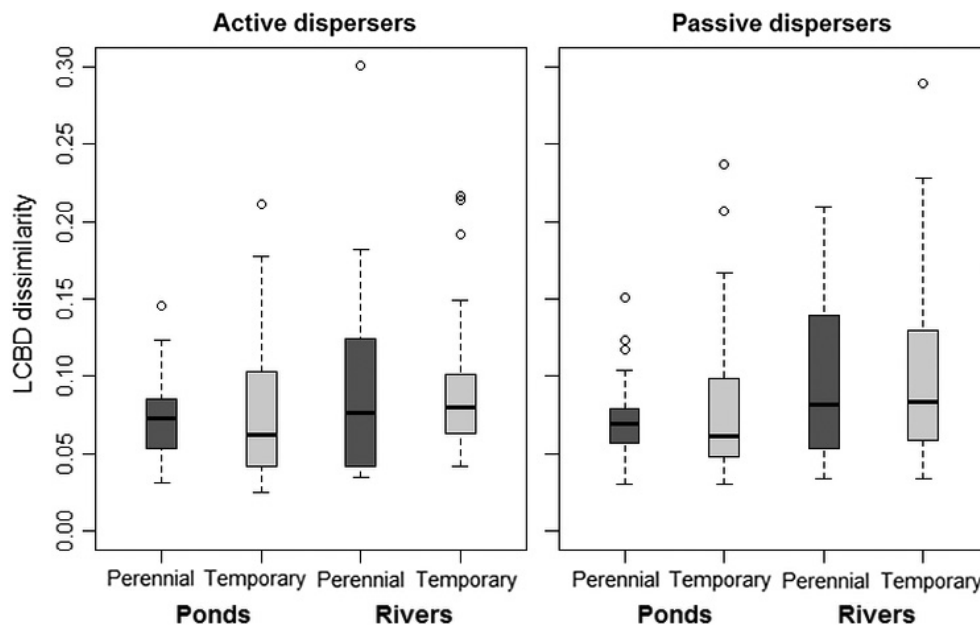


Fig. 5. Local contributions to beta diversity (LCBD) for dissimilarity differences in perennial and temporary river and pond ecosystems. Graphical representation as in Fig. 2.

Phylogenetic relatedness.—Responses of phylogenetic relatedness to drying disturbance also support the idea that hydrological connectivity may mediate community responses to drying disturbance: Communities of drying sites were more clustered than those from perennial sites, and the effect of drying on phylogenetic relatedness was smaller in lotic ecosystems. One widely recognized mechanism for phylogenetic clustering is environmental filtering on shared physiological tolerances (trait conservatism; Cavender-Bares et al. 2009). For example, previous studies have demonstrated that macroinvertebrate communities in temporary wetlands are more phylogenetically related under harsher environmental conditions, such as in arid environments (Ruhi et al. 2013a). Environmental filtering (e.g., via drying disturbance) may thus have stronger effects on lentic than on lotic communities, filtering out species from the regional species pool (Chase 2007).

Beta diversity.—In contrast to alpha diversity and phylogenetic relatedness, water permanence did not strongly influence the contributions of local communities to the turnover and richness components of beta diversity. This may be due to the interacting influences of water permanence, ecosystem type, and dispersal abilities (Heino et al. 2014, Ruhi et al. 2017). Dispersal homogenization, which may lead to larger contributions of richness gradients (nestedness) to beta diversity, can be caused by high levels of hydrological connectivity, water permanence, or dispersal abilities. Similarly, colonization and priority effects, which may result in taxa turnover being the primary driver of beta diversity, can dominate when hydrological connectivity, water permanence, or dispersal abilities are low. Both turnover and richness gradients may contribute to community dissimilarity across the small spatial scales of the focal datasets (10–100 km²) and drying disturbance may not alter this balance. A recent study from Australian rock pools also found similar contributions of turnover and richness gradients to beta diversity (Brendonck et al. 2015). However, they observed that richness gradients were clearly related to hydrological stability in terms of frequency and length of dry period, suggesting a strong importance of environmental filtering of drying-intolerant taxa. An analysis of New Zealand river communities also revealed differences in the importance of

environmental compared with spatial variables that were related to the frequency and intensity of disturbance (Campbell et al. 2015). This variability in space and time of the responses of taxonomic composition to disturbance may have hindered the detection of clear patterns in the relative importance of richness and turnover gradients to beta diversity.

Differing responses to drying disturbance between active and passive dispersers

Although there were differences in community responses to drying between lentic and lotic ecosystems, there was not a clear effect of dispersal mode (i.e., active compared with passive dispersers). This finding may be surprising given the number of studies reporting the importance of dispersal in structuring communities and metacommunities (e.g., De Bie et al. 2012, Cañedo-Argüelles et al. 2015). However, many previous studies were focused only on perennial habitats whose taxa may differ in terms of resistance and resilience strategies from drying habitats (De Bie et al. 2012, Liu et al. 2013). Communities of temporary aquatic habitats may rely more on resistance strategies (e.g., resting eggs of Chironomidae), and thus, dispersal mode may play a secondary role. Additionally, differences between active and passive dispersers are often reported at relatively large spatial scales (>100 km²; De Bie et al. 2012, Cañedo-Argüelles et al. 2015). In contrast, differences between passive and active dispersers were not significant at a small spatial scale (4 km radius) for ponds from England (Rundle et al. 2002). Thus, dispersal limitation may play a larger role at larger spatial scales than those examined in the present study (1–100 km²). Finer classification of taxa dispersal mode and further knowledge about macroinvertebrate dispersal behavior are readily available for some highly studied taxonomic groups but have not been quantified for most taxa. This information would help disentangle the importance of dispersal processes in structuring metacommunities (Cañedo-Argüelles et al. 2015, Kärnä et al. 2015, Li et al. 2016).

Conservation implications

Drying is a natural disturbance in rivers and ponds across all biomes (Williams 2006). However, intensifying climate variability and

appropriation of freshwater resources are increasing the frequency of drying in some aquatic ecosystems (e.g., rivers; Vörösmarty et al. 2010). Additionally, hydroclimatic models predict increased aridity and extreme events in many regions (Milly et al. 2005, Ledger et al. 2011, Lin et al. 2016), thus augmenting the frequency, magnitude, and duration of drying disturbance in both lentic and lotic ecosystems and potentially causing extinctions of endemic species (Bogan et al. 2015). Increased aridity may also make overland dispersal more perilous or difficult for aquatic organisms traveling across increasingly harsher terrestrial matrices. Climate-dependent responses of aquatic communities to environmental filtering have been reported, for example, from temporary wetlands (Ruhi et al. 2013a) and desert springs (Cushing and Gaines 1989). The findings of the present study imply that these hydroclimatic changes may make aquatic communities more reliant on dispersal and remaining hydrological connectivity in the future, as suggested by Vanschoenwinkel et al. (2013). Although lotic ecosystems may suffer less from fragmentation than lentic ecosystems, climate-induced transitions from perennial to temporary habitats (e.g., Bogan and Lytle 2011) will decrease habitat connectivity at the landscape level even in lotic ecosystems (Jaeger et al. 2014). Therefore, understanding the dispersal abilities of aquatic species and preserving dispersal corridors will be essential to maintaining community dynamics across increasingly dry and fragmented landscapes.

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