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Response of stream fungi on decomposing leaves to experimental drying

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Abstract

Climate change may lead to increased droughts in the future, which in turn may lead to increased periods of stream drying. We conducted an experiment to test the effects of drying on fungal communities and microbial activity on decaying leaves from a stream. Our experimental setup included immersion of maple leaf cores for 2 weeks in a small stream to allow for the colonization of microbes. Leaves were then subjected for 2 weeks to four treatments: one control, where leaves stayed immersed in the stream, and three drying treatments in different settings (field, lab, and oven). Leaves were then returned to sterile water for 2 weeks of recovery. Microbial respiration declined after all drying treatments compared to the control, with the oven-dried leaves taking the longest time to recover. All drying treatments had similar respiration to each other and the control after 2 weeks of immersion recovery. Fungal communities on the leaves were assessed by polymerase chain reaction amplification of fungal DNA from leaves followed by denaturing gradient gel electrophoresis (DGGE). Most treatments had very similar communities based on phylotypes from DGGE, with little change during drying and recovery compared to immersion controls. However, the oven-dried leaves had a very different community developing during recovery. There were no differences in diversity or richness of DGGE phylotypes among treatments after recovery. Overall, the fungal communities, in our experiment, appeared resilient to the effects of short-term drying, with little change to community structure and relatively fast recovery in activity after rewetting.

KEYWORDS
climate change, desiccation, drought, function, microbes

1 | INTRODUCTION

Litter breakdown is a key ecosystem process, supporting food webs in most streams (Wallace, Eggert, Meyer, & Webster, 1997) and can be used as a measure of stream health (Gessner & Chauvet, 2002; Young, Matthaei, & Townsend, 2008). The process is mediated by two biotic players: microbes and invertebrates. Microbes colonize leaf litter, mineralize some carbon and nutrients, and make leaf litter more palatable to invertebrates (Arsuffi & Suberkropp, 1984). Shredding invertebrates consume the leaf litter and associated microbes, mineralizing some carbon and nutrients and also converting coarse particulate organic matter to fine particulate organic matter (Niyogi, Lewis, & McKnight, 2001). Fungi are considered to be the main microbial decomposers in streams in the early stages of litter breakdown (Pascoal & Cassio, 2004; Suberkropp & Weyers, 1996). Stream fungi, especially aquatic hyphomycetes, can be affected by a variety of stressors in streams, including low pH and toxic chemicals (reviewed in Gessner & Chauvet, 2002; Krauss et al., 2011). In this study, we examined the response of fungal communities in streams to experimental drying.

With climate change, streams may experience increased periods of reduced or no flow following extended droughts. Streams in the central United States are especially susceptible to stress from reduced streamflow and possible stream drying (Covich et al., 1997). Furthermore, seasonal flow variability is expected to increase with larger peak flow events and more time with low or no flow in many streams (Chien, Yeh, & Knouft, 2013; Mulholland et al., 1997). This greater range of flow may cause leaf litter in streams to be exposed to air during low flow and then immersed again later during high flow.

Many streams currently dry out each year for varying lengths of time. These intermittent rivers and ephemeral streams (IRES) commonly have different biota from perennial streams (Larned, Datry, & Robinson, 2007), as well as different rates of ecosystem processes, including litter breakdown (Datry, Corti, Claret, & Philippe, 2011; Gonçalves, Lírio, Graça, & Canhoto, 2016). Stream drying usually lowers rates of litter breakdown because of effects on invertebrates and microbes that consume the organic matter (Datry et al., 2011).

Fewer studies have focused on fungi and their activity in intermittent streams or under drying stress. Maamri, Bärlocher, Pattee, and Chergui (2001) compared litter breakdown and its main microbial agents in permanent and intermittent reaches of the same stream. Litter breakdown was significantly slower in the intermittent stream sections and during dry periods, which shows that drought may change the functioning of the ecosystems. Schlief and Mutz (2011) noted slow breakdown and reduced microbial activity in a stream that became fragmented during a severe drought. Duarte, Mora-Gómez, Romaní, Cássio, and Pascoal (2017) found that breakdown rate and enzyme activities decreased in a stream following emersion.

Several recent studies have used drying experiments to examine effects on stream fungi and leaf breakdown. Bruder, Chauvet, and Gessner (2011) found that drying created immediate effects on fungi as well as delayed effects after 3 weeks of recovery in water. Foulquier, Artigas, Pesce, and Datry (2015) examined the frequency of emersion periods on stream fungi and bacteria during a 4-week experiment and found some effects of drying but not frequency. Arroita, Flores, Larrañaga, Chauvet, and Elosegi (2018) conducted an experiment with several drying treatments based on the timing of emersion followed by a 4-week recovery period. They found some effects of drying on fungi, but good recovery of microbial activity during the immersion recovery. Finally, Gonçalves, Simões, Bärlocher, and Canhoto (2019) examined microbial activity and fungal communities during an experiment that tested the effects of drying and salinization. They found some effects of drying on fungi, including changes to community structure based on different drying treatments.

In this study, we examined the effects of four drought treatments on fungal community structure and measured the respiration rates to compare microbial activity under drought stress and during recovery in water. The drought treatments varied from controls (continuous immersion) to extreme drying (in an oven). We used a molecular method (Nikolcheva, Cockshutt, & Bärlocher, 2003) to compare fungal communities on leaves across the treatments. We hypothesized that drought stress would alter the fungal communities and lead to lower diversity compared to wet controls, with more extreme drying leading to greater effects. Similarly, we predicted that microbial activity would be low after a drought but recover after reimmersion in water; extreme drying was expected to lead to larger declines and slower recovery of activity.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study site was a second-order stream located in Rolla, MO (37°96′36″N, −91°77′99″W) in a nature preserve (Audubon Trails nature area). Discharge at the study site is usually about 5–15 L/s during baseflow. The streambed is characterized by riffle-pool morphology and consists of gravels and cobble-sized rocks. The riparian vegetation at the study site is composed mainly of deciduous trees, including red oak, sycamore, and others. Wood and leaf litter are scattered throughout the streambed, particularly in the slow-moving parts of the stream.

2.2 | Leaf colonization and experimental drying

Maple leaves (*Acer saccharum*) were collected after abscission in autumn and air-dried in the lab. Before the experiment, leaves were autoclaved in deionized water for sterilization and cut into cores using a corer (1.8-cm diameter). About 150 leaf cores were placed in litterbags with a mesh size of 5 mm and placed in the stream in winter. Leaf cores were spread out in the mesh bags to allow them to have full exposure to stream water, and a large mesh size allowed ample contact with flowing water and dissolved oxygen. Leaf cores were collected after 2 weeks of colonization, and we measured microbial respiration and initial fungal community composition (described below). Next, we separated the remaining leaf cores into four different treatments for the next 2 weeks: (a) wet in the stream as a control, (b) exposed to air but covered on the stream bank, (c) air-dried and exposed to sunlight in the lab, and (d) oven-dried (50°C) in the lab (Figure 1). We selected these different treatments to test a gradient of drying conditions on stream fungi, from less stressful (field-dried) to extreme (oven-dried). Two weeks of drying was used

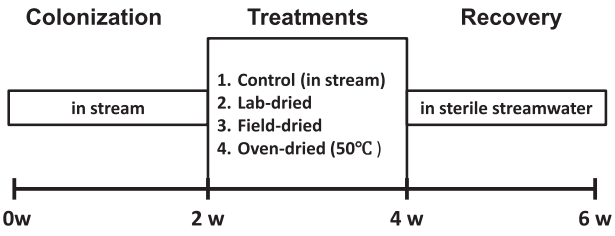

FIGURE 1 Overview of experimental design, with 2-week periods of colonization, drying treatment, and recovery in water, for a total of 6 weeks

because that timing is consistent with short periods of stream drying during droughts in the area. Next, leaf cores of each treatment were placed in 50 ml of sterilized stream water in flasks and incubated on a shaker table at 70 rpm (in the lab at 20°C) for the following 2 weeks of "recovery." This included the control leaves from the stream, which were brought to the lab and also added to sterilized stream water in flasks. The rate of microbial respiration on the leaf cores was measured after 0, 0.167 (4 hr), 1, 3, 7, and 14 days of recovery. Leaf cores (three replicate samples of three-leaf cores each) of the treatments were taken for DNA analysis of fungal communities on days 7 and 14 of recovery. An additional set of cores were taken after the initial 2-week colonization time to serve as starting points for communities before drying.

2.3 | Microbial respiration analysis

In the laboratory, microbial respiration rates were used as a measure of microbial activity following methods described in Niyogi, Harding, and Simon (2013). On each collection date, oxygen consumption was measured for four replicate samples for each treatment, where three-leaf cores for each replicate were enclosed in 26-ml vials that contained sterilized stream water. Each vial was gently stirred during the incubations with small stir rods on a magnetic stir plate. Preliminary results showed that the oxygen uptake was linear during the course of the incubations. The respiration rates were measured over 4 hr from changes in dissolved oxygen after correcting for oxygen changes in control vials containing only sterilized stream water. Microbial respiration is reported as micrograms of O_2 consumed per mg of the ash-free dry mass of leaf per hour.

2.4 | Fungal communities

Fungal communities were examined using denaturing gradient gel electrophoresis (DGGE) following the standard molecular methods outlined in Nikolcheva and Bärlocher (2005), with some minor modifications as described by Niyogi, Cheatham, Thomson, and Christiansen (2009). DNA of leaf cores was extracted with an UltraClean Soil DNA Isolation Kit (MoBio Laboratories, Inc., Carlsbad, CA) following the manufacturer instructions. From the DNA extract, fungal DNA was amplified using fungal-specific primers ITS3GC, which was modified by adding a 40-bp GC tail on the 5′ end of ITS3 (5′-CGCCCGCCGCGCCCCGCGCCCGGCCCGCCGCCCCCG CCCCGCATCGATGAAGAACGCAGC-3′) and ITS4 (5′-TCCTCCGC TTATTGATATGC-3′). The amplifications were performed with illustra Ready-To-Go PCR Beads (GE Healthcare, Piscataway, NJ). The amplification program started with a 2-min initial denaturation at 95°C, 35 cycles of denaturation for 30 s at 95°C, primer annealing for 30 s at 55°C, an extension for 1 min at 72°C, and final extension for 5 min at 72°C. Thompson, Marcelino, and Polz (2002) suggested that heteroduplexes can form with mismatched strands of similar DNA sequences during the latter stages of polymerase chain reaction (PCR), and lead to extra bands on DGGE gels. Consequently, we used a "reconditioning PCR" step to reduce heteroduplex formation (Thompson et al., 2002). The protocols used a dilution of the initial PCR product and ran a low cycle number reamplification with fresh primers and PCR reagents.

The reconditioning PCR products were analyzed by DGGE with the DCode Universal Mutation Detection System (Bio-Rad, Hercules, CA). The products (20 μl) were loaded on 8% (wt/vol) acrylamide gel in 1× Tris-acetic acid EDTA (TAE) buffer through a 30–70% denaturant gradient (100% denaturant has 7 M urea and 40% foramide). Gels were run in 1× TAE at 60 V and 60°C for 16 hr, and stained with SYBR Green for 45 min followed by destaining with deionized water for 15 min and imaged for analysis. The fungal community composition of samples was assessed based on the banding patterns of DGGE bands, where each band represents a different phylotype. Band intensity was measured by gel analysis using ImageAide software and the band intensity was used to determine the community composition of different phylotypes.

2.5 | Statistical analysis

Parametric statistics were used to compare rates of microbial respiration and values for Shannon–Wiener diversity across treatments, with the use of SigmaStat software (ver 4.0). After confirming normal distributions and homogeneity of variance, analysis of variance (ANOVA) was used for testing differences based on drying treatment, followed by pair-wise comparisons using the Tukey tests. Nonmetric multidimensional scaling (NMDS) was conducted with PC-ORD (ver 7.08) to ordinate the fungal community data (from DGGE phylotypes) into fewer dimensions. The ordination was based on Sorensen's distances among composition data (proportions for each sample) after arcsine-square root transformation. Our two-dimensional NMDS solution had a stress value of 0.14, indicating a good representation of the community differences in the analysis. PERMANOVA was used to check for differences in fungal communities (based on DGGE phylotypes) from different drying treatments.

3 | RESULTS

3.1 | Experimental setup

Leaf litter was colonized by microbes during 2 weeks of immersion in the stream, which had a discharge of about 15 L/s during the colonization period. During the differential treatments of the following 2 weeks, the leaf cores underwent varying degrees of drying. Leaf cores in the lab treatment (air-dried in sunlight) and oven treatment dried to constant mass over 24 hr and remained dried for 2 weeks. The field-dried treatment led to dried leaf cores during the first week, but high rainfall during the second week let to the cores being moist. The control treatment of leaf cores in the stream remained wet in flowing water for all 2 weeks.

3.2 | Microbial activity

Microbial respiration was the highest on the continuously immersed leaves during the 2 weeks of recovery time (Figure 2). Leaves from all drying treatments (field, lab, and oven) had significantly lower respiration rates than the control leaves for the first 3 days of recovery in stream water in the lab ($n = 4$ replicates per treatment for each time; $p < .05$ for all comparisons). The field-dried leaves had slightly higher respiration than the lab and oven-dried leaves at the start of recovery. After 7 days of immersion recovery, the respiration rates of the field and lab-dried leaves approached the rate of the continuously immersed leaves (no significant difference among these treatments, $p > .05$). The oven-dried leaves had the lowest respiration rate throughout the recovery period. This rate was significantly lower than the control leaves after 7 days of recovery ($p = .016$), but it was not significantly different from other treatments at the final, 14-day recovery trial ($p = .151$).

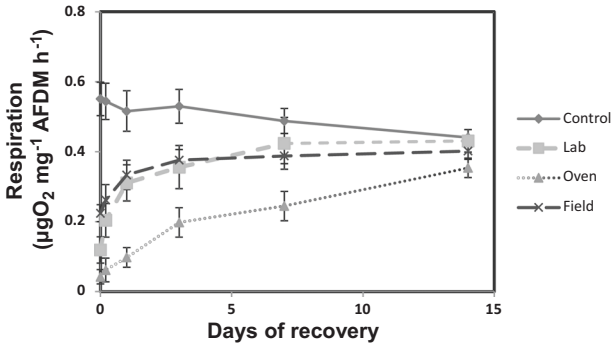

FIGURE 2 Microbial respiration during the 2 weeks of recovery after drying treatments. The four treatments are listed in the key. The control treatment leaves remained immersed in the stream for the 2 weeks of treatments; the drying treatments were exposed to air for 2 weeks. Values are means ± 1 SE for four replicate samples. AFDM, ash-free dry mass; SE, standard error

3.3 | Fungal communities by DDGE

The DGGE analysis showed similar and dissimilar fungal phylotypes among the different treatments (Figure 3). The control, field-dried, and lab-dried leaves all had very similar fungal communities, both among replicate samples and among these three treatments after the 2-week recovery period. The only treatment that had dissimilar communities to the others was the oven-dried treatment. Very few of the phylotypes from DGGE samples from the other treatments occurred in the oven-dried treatment leaves, and none were highly abundant (based on DNA band intensity on DGGE gel as in Figure 3). There was no significant difference in Shannon–Wiener diversity among the treatments after recovery (Figure 4; $p = .75$); the richness of phylotypes from DGGE analysis also did not differ among treatments ($p = .46$). An NMDS ordination of the phylotype communities from the DGGE analysis showed that the oven-dried samples were very different from the other samples, which were quite similar (Figure 4). PERMANOVA revealed a significant difference in the fungal communities from the oven-dried treatment compared to the other treatments ($p < .01$) (Figure 5).

4 | DISCUSSION

Our study had several limitations, including relatively few replicate samples for most analyses and a lack of sequencing to identify fungal taxa. However, our simple experiment still provided interesting patterns in fungal responses to drying. Rates of microbial activity after reimmersion recovered within a week for most drought treatments, with the exception of the harshest, oven-dried treatment. Similarly, fungal communities were not altered greatly by drying in the field or lab, and only the oven-dried treatment led to large changes in the fungal phylotypes on the leaves. Interestingly, the different fungal communities that recovered in the oven-dried treatment still contributed to respiration rates that were similar to other treatments after 2 weeks of recovery.

Most other studies have found a slower breakdown of leaves in streams that are dry, whether intermittent or ephemeral. Invertebrates that consume leaves, shredders, often contribute significantly to leaf breakdown, so if these animals are lost upon drying, rates will be much lower (Datry et al., 2011; Ledger, Harris, Armitage, & Milner, 2012; Palmia et al., 2019). Microbes, the other biological player in leaf breakdown, are also usually less active under dry conditions as well. Under varying hydrologic conditions, microbial activity is

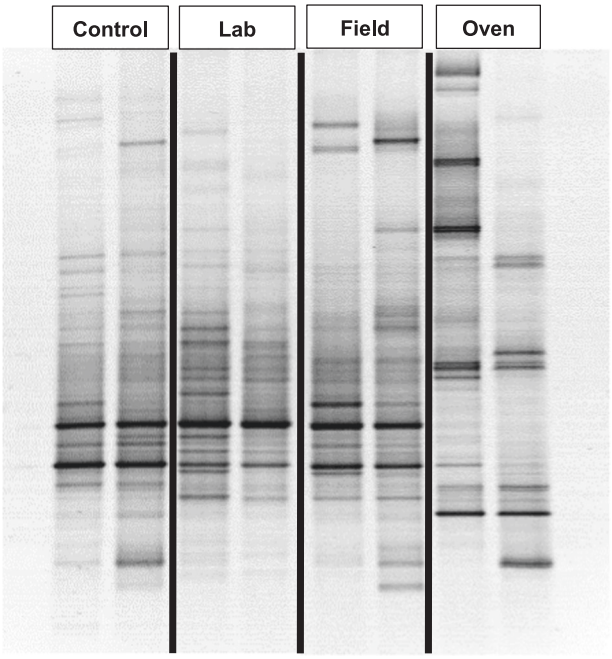

FIGURE 3 Denaturing gradient gel for a subset of samples after 2 weeks of immersion recovery from drying treatments. The two lanes for each treatment are replicate DNA samples following extraction and polymerase chain reaction from treatment leaves. Each band represents a different phylotype of fungi for the sample

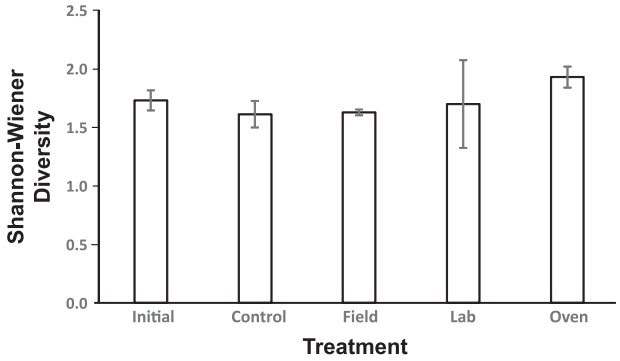

FIGURE 4 Shannon–Wiener diversity of fungal communities from denaturing gradient gel electrophoresis analysis for four treatments after recovery and also the initial community after 2 weeks of colonization. Values are means ± 1 standard error for three replicate samples for each treatment

related to the time of immersion, with longer immersion time leading to faster breakdown (Datry et al., 2011; Langhans & Tockner, 2006).

Several studies have also used drying experiments to test the effects of drying on stream fungi. Foulquier et al. (2015) examined leaf breakdown with experimental drying of varying frequency over a 4-week period. They found lower activity and fungal biomass in all treatments with drying exposure compared to immersed controls, but they did not examine recovery from emersion. Our study focused on the recovery time for microbial activity after drying and found that it was quite short (less than 1 week) for natural rates of drying (our field and lab treatments). Bruder et al. (2011) also examined drying regimes on fungal responses and included an oven-dried treatment like ours. This harsh treatment led to lower fungal biomass in their study, even after 3 weeks of recovery in a stream. Thus, their study revealed slower recovery compared to our results. Arroita et al. (2018) examined microbial respiration on leaves under varying drying regimes for 2 weeks with a 4-week recovery. They found that microbial respiration had temporary declines compared to controls,

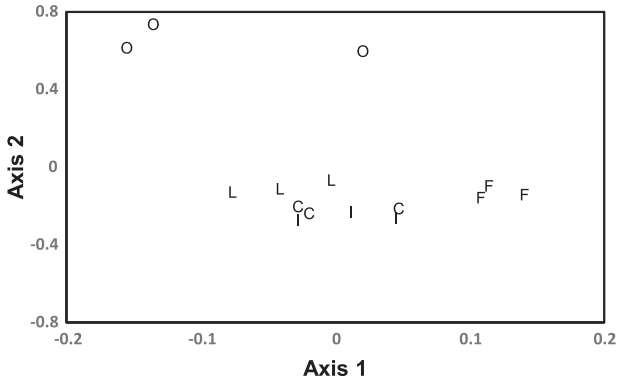

FIGURE 5 Nonmetric multidimensional scaling ordination plot for fungal communities based on phylotypes from denaturing gradient gel electrophoresis gels. Each treatment had three replicate samples, with letters as markers indicating treatments: C is the control, F is field-dried, L is lab-dried, O is oven-dried, and I is the initial communities after 2 weeks of colonization

but all treatments had recovered after 2 weeks and 4 weeks of recovery. However, they did find larger declines in ergosterol and sporulation rates under some drying treatments.

Mora-Gómez, Duarte, Cássio, Pascoal, and Romaní (2018) examined the effects of emersion duration (0–3 weeks) on litter from a perennial stream. Emersion duration had some effects on microbial responses, especially breakdown rate. Finally, Gonçalves et al. (2019) recently conducted a study on leaf litter microbes under flow intermittency and salinization. Like our study, they had three drying treatments based on rate (very slow to abrupt), with longer time of drying (up to 5 weeks) followed by 3 weeks of recovery. They did not find significant differences in respiration after recovery, but there were differences in fungal biomass (ergosterol) and sporulation rates, with lower values for the drying treatments. They also found changes in the community composition of fungi across drying treatments based on conidia analysis. Our results differed somewhat because we saw fungal community changes only in our extreme drying treatment. However, both their study and ours found that functional redundancy can occur with stream fungi on leaves.

Fewer studies have examined fungal communities under drying stress. Chauvet, Cornut, Sridhar, Selosse, and Bärlocher (2016) reviewed studies that examined the response of aquatic hyphomycetes to dry conditions; several studies have found that many taxa could survive some degree of drying, although activity and sporulation would often be reduced. Romaní et al. (2017) reviewed data on microbial communities, including bacteria, fungi, and protists, in IRES. They noted that many taxa can survive in IRES habitats, including some aquatic hyphomycetes. We were surprised that our drying treatments that reflect natural conditions (field and lab-dried leaves) had very similar fungal communities compared to the immersed control leaves; in other words, the fungal communities showed little change from drying stress. Diversity of fungal communities did not decline in our experiment as we predicted. It is likely that our drying time in our experiment, only 2 weeks in duration, was not long enough to lead to major changes in the community. Our oven-dried community was very different from all the other treatments, indicating that extremely harsh drying (in 50°C oven) can kill many fungal taxa, and allow very different taxa to become dominant on the leaves (Figure 3).

Foulquier et al. (2015) used a molecular method, ARISA fingerprints, to examine the fungal communities in their drying experiment. They found some differences based on flow regime for two sections of a river with perennial versus intermittent flow, but less difference based on the frequency of drying events. Mora-Gómez et al. (2018) used the same method as our study (DGGE) and found differences in fungal communities over time, but less change among their drying treatments. They, along with Gonçalves et al. (2019), examined conidia of aquatic hyphomycetes in their studies, and both saw some changes in fungal communities with drying stress.

In summary, fungal communities in our experiment were able to tolerate 2 weeks of drying in the field or lab, which would be similar to drought conditions leading to a temporary cessation of flow and emersion of decomposing leaves. Only an extreme oven-drying

treatment led to major changes based on DGGE analysis of fungal DNA from leaves. Microbial respiration on decomposing leaves did decline with drying, but also recovered quickly and was similar to the immersed controls after 2 weeks of recovery.

We were surprised by the resilience of the fungal community and microbial activity seen in our experiment. However, more severe drying with drought, related to longer emersion, temperature stress, or UV exposure, could certainly affect community structure and activity of microbes in streams. Intermittent rivers will likely increase in the future with climate change, and these important habitats are important to carbon cycling even on a global scale (Datry et al., 2018). Greater periods of emersion for these streams will most likely slow the conversion of energy from litter into stream food webs. Furthermore, stream drying will likely directly affect animal communities, including shredding invertebrates, that also play a key role in litter breakdown. Microbial communities may be more tolerant to stream drying, and recover more quickly, than animals. In these drying streams, which may become more common with climate change, microbial processing of leaf litter may become the main mechanism for breakdown at the expense of animals and other components of a more complex food web.

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REFERENCES

Arroita, M., Flores, L., Larrañaga, A., Chauvet, E., & Elosegi, A. (2018). Hydrological contingency: Drying history affects aquatic microbial decomposition. *Aquatic Sciences*, *80*, 31.

Arsuffi, T. L., & Suberkropp, K. (1984). Leaf processing capabilities of aquatic hyphomycetes: Interspecific differences and influence on shredder feeding preference. *Oikos*, *42*, 144–154.

Bruder, A., Chauvet, E., & Gessner, M. O. (2011). Litter diversity, fungal decomposers and litter decomposition under simulated stream intermittency. *Functional Ecology*, *25*, 1269–1277.

Chauvet, E., Cornut, J., Sridhar, K. R., Selosse, M.-A., & Bärlocher, F. (2016). Beyond the water column: Aquatic hyphomycetes outside their preferred habitat. *Fungal Ecology*, *19*, 112–127.

Chien, H., Yeh, P. J.-F., & Knouft, J. H. (2013). Modeling the potential impacts of climate change on streamflow in agricultural watersheds of the Midwestern United States. *Journal of Hydrology*, *491*, 73–88.

Covich, A. P., Fritz, S. C., Lamb, P. J., Marzolf, R. D., Matthews, W. J., Poiani, K. A., … Winter, T. C. (1997). Potential effects of climate change on aquatic ecosystems of the Great Plains of North America. *Hydrological Processes*, *11*, 993–1021.

Datry, T., Corti, R., Claret, C., & Philippe, M. (2011). Flow intermittence controls leaf litter breakdown in a French temporary alluvial river: The "drying memory". *Aquatic Sciences*, *73*, 471–483.

Datry, T., Foulquier, A., Corti, R., Von Schiller, D., Tockner, K., … Zoppini, A. (2018). A global analysis of terrestrial plant litter dynamics in non-perennial waterways. *Nature Geoscience*, *11*, 497–503.

Duarte, S., Mora-Gómez, J., Romaní, A. M., Cássio, F., & Pascoal, C. (2017). Responses of microbial decomposers to drought in streams may depend on the environmental context. *Environmental Microbiology Reports*, *9*, 756–765.

Foulquier, A., Artigas, J., Pesce, S., & Datry, T. (2015). Drying responses of microbial litter decomposition and associated fungal and bacterial communities are not affected by emersion frequency. *Freshwater Sciences*, *34*, 1233–1244.

Gessner, M. O., & Chauvet, E. (2002). A case for using litter breakdown to assess functional stream integrity. *Ecological Applications*, *12*, 498–510.

Gonçalves, A. L., Lírio, A. V., Graça, M. A. S., & Canhoto, C. (2016). Fungal species diversity affects leaf decomposition after drought. *International Review of Hydrobiology*, *101*, 78–86.

Gonçalves, A. L., Simões, S., Bärlocher, F., & Canhoto, C. (2019). Leaf litter microbial decomposition in salinized streams under intermittency. *Science of the Total Environment*, *653*, 1204–1212.

Krauss, G. J., Solé, M., Krauss, G., Schlosser, D., Wesenberg, D., & Bärlocher, F. (2011). Fungi in freshwaters: Ecology, physiology and biochemical potential. *FEMS Microbiology Reviews*, *35*, 620–651.

Langhans, S. D., & Tockner, K. (2006). The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, northeastern Italy). *Oecologia*, *147*, 501–509.

Larned, S. T., Datry, T., & Robinson, C. T. (2007). Invertebrate and microbial responses to inundation in an ephemeral river reach in New Zealand: Effects of preceding dry periods. *Aquatic Sciences*, *69*, 554–567.

Ledger, M. E., Harris, R. M., Armitage, P. D., & Milner, A. M. (2012). Climate change impacts on community resilience: Evidence from a drought disturbance experiment. *Advances in Ecological Research*, *46*, 211–258.

Maamri, A., Bärlocher, F., Pattee, E., & Chergui, H. (2001). Fungal and bacterial colonisation of Salix pedicellata leaves decaying in permanent and intermittent streams in Eastern Morocco. *International Review of Hydrobiology*, *86*, 337–348.

Mora-Gómez, J., Duarte, S., Cássio, F., Pascoal, C., & Romaní, A. M. (2018). Microbial decomposition is highly sensitive to leaf litter emersion in a permanent temperate stream. *Science of the Total Environment*, *621*, 486–496.

Mulholland, P. J., Best, G. R., Coutant, C. C., Hornberger, G. M., Meyer, J. L., Robinson, P. J., … Wetzel, R. G. (1997). Effects of climate change on freshwater ecosystems of the south-eastern United States and the Gulf Coast of Mexico. *Hydrological Processes*, *11*, 949–970.

Nikolcheva, L. G., & Bärlocher, F. (2005). Molecular approaches to estimate fungal diversity. II. Denaturing gradient gel electrophoresis (DGGE). In M. A. S. Graça, F. Bärlocher & M. O. Gessner (Eds.), *Methods to study litter decomposition: A practical guide* (pp. 177–183). Dordrecht, The Netherlands: Springer.

Nikolcheva, L. G., Cockshutt, A. M., & Bärlocher, F. (2003). Determining diversity of freshwater fungi on decaying leaves: Comparison of traditional and molecular approaches. *Applied and Environmental Microbiology*, *69*, 2548–2554.

Niyogi, D. K., Cheatham, C. A., Thomson, W. H., & Christiansen, J. M. (2009). Litter breakdown and fungal diversity in a stream affected by mine drainage. *Fundamental and Applied Limnology*, *175*, 39–48.

Niyogi, D. K., Harding, J. S., & Simon, K. S. (2013). Organic matter breakdown as a measure of stream health in New Zealand streams affected by acid mine drainage. *Ecological Indicators*, *24*, 510–517.

Niyogi, D. K., Lewis, W. M., & McKnight, D. M. (2001). Litter breakdown in mountain streams affected by mine drainage: Biotic mediation of abiotic controls. *Ecological Applications*, *11*, 506–516.

Palmia, B., Bartoli, M., Laini, A., Bolpagni, R., Ferrari, C., & Viaroli, P. (2019). Effects of drying and re-wetting on litter decomposition and nutrient recycling: A manipulative experiment. *Water*, *11*, 708.

Pascoal, C., & Cassio, F. (2004). Contribution of fungi and bacteria to leaf litter decomposition in a polluted river. *Applied and Environmental Microbiology*, *70*, 5266–5273.

Romaní, A. M., Chauvet, E., Febria, C., Mora-Gómez, J., Risse-Buhl, U., Timoner, X., … Zeglin, L. (2017). The biota of intermittent rivers and ephemeral streams: Prokaryotes, fungi, and protozoans, *Intermittent rivers and ephemeral streams: Ecology and management* (pp. 161–188). London, UK: Academic Press.

Schlief, J., & Mutz, M. (2011). Leaf decay processes during and after a supra-seasonal hydrological drought in a temperate lowland stream. *International Review of Hydrobiology*, *96*, 633–655.

Suberkropp, K., & Weyers, H. (1996). Application of fungal and bacterial production methodologies to decomposing leaves in streams. *Applied and Environmental Microbiology*, *62*, 1610–1615.

Thompson, J. R., Marcelino, L. A., & Polz, M. F. (2002). Heteroduplexes in mixed template amplifications: Formation, consequence and elimination by 'reconditioning PCR'. *Nucleic Acids Research*, *30*, 2083–2088.

Wallace, J. B., Eggert, S. L., Meyer, J. L., & Webster, J. R. (1997). Multiple trophic levels of a forested stream linked to terrestrial litter inputs. *Science*, *277*, 102–104.

Young, R. G., Matthaei, C. D., & Townsend, C. R. (2008). Organic matter breakdown and ecosystem metabolism: Functional indicators for assessing river ecosystem health. *Journal of North American Benthological Society*, *27*, 605–625.

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