

A global analysis of terrestrial plant litter dynamics in non-perennial waterways

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101

102 **Perennial rivers and streams make a disproportionate contribution to global carbon (C)**

103 **cycling. However, the contribution of intermittent rivers and ephemeral streams, which**

104 **sometimes cease to flow and can dry completely, is largely ignored although they**
105 **represent over half the global river network. Substantial amounts of terrestrial plant**
106 **litter accumulate in dry riverbeds and, upon rewetting, this material can undergo rapid**
107 **microbial processing. We present the results of a global research collaboration which**
108 **collected and analysed terrestrial plant litter from 212 dry riverbeds spanning major**
109 **environmental gradients and climate zones. We assessed litter decomposability by**
110 **quantifying the litter C-to-nitrogen ratio (C:N) and oxygen (O₂) consumption in**
111 **standardised assays and estimated potential short-term CO₂ emissions during rewetting**
112 **events. Aridity, cover of riparian vegetation, channel width, and dry phase duration**
113 **explained most variability in the quantity and decomposability of plant litter in**
114 **intermittent rivers and ephemeral streams. Our estimates indicate that a single pulse of**
115 **CO₂ emission upon litter rewetting contribute up to 10% of daily CO₂ emission from**
116 **perennial rivers and stream, particularly from temperate climates. This implies that the**
117 **contributions of intermittent rivers and ephemeral streams should be included in global**
118 **C cycling assessments.**

119

120 Decomposition of terrestrial plant litter is an essential, biosphere-scale ecosystem process¹. Of
121 120 Pg of organic C produced by terrestrial plants annually, about half is respired by the
122 plants but only a small fraction is removed by herbivores, so that up to 60 Pg enter the dead
123 organic matter pool^{1,2}. Fresh waters make a disproportionate contribution to global C cycling
124 through terrestrial plant litter (TPL) decomposition and atmospheric CO₂ emissions^{3,4}. This
125 contribution is particularly apparent in perennial rivers and streams, where water and nutrient
126 availability stimulate rapid decomposition by microbes and invertebrate detritivores^{1,3,5}. TPL
127 deposited in fresh waters, and the release of its decomposition products, are critical energy
128 sources that support food webs and ecosystem processes, including key C cycling pathways^{1,5}.

129

130 A major shortcoming of current estimates of the contribution of rivers and streams to global C
131 cycling^{3,6,7} is the omission of intermittent rivers and ephemeral streams (IRES), in which
132 drying and rewetting events create ecosystems that transition between terrestrial and aquatic
133 phases^{8,9,10}. IRES are widespread ecosystems draining a large proportion of terrestrial biomes
134 across all continents and climate types^{9,12}. Moreover, IRES are increasing in extent due to
135 global change^{8,13}. During the dry phase, TPL deposited on the riverbed accumulates,
136 decomposing only slowly through photodegradation and terrestrial decomposer activity^{14,15}.
137 Then, when flow resumes, the accumulated material is mobilised and transported
138 downstream^{16,17} (**Supplementary Material 1**). Concentrations of particulate and dissolved
139 organic matter in advancing wetted fronts exceed baseflow concentrations by several orders
140 of magnitude¹⁶. IRES have therefore been conceptualised as punctuated biogeochemical
141 reactors⁹.

142

143 To understand the role of IRES in global C cycling, global-scale data are needed to
144 characterise the variables controlling TPL accumulation in dry channels and its
145 decomposability upon flow resumption. Climate influences the type and productivity of
146 riparian vegetation¹⁸ and the flow regimes of IRES^{8,13}. Channel topography and flow
147 conditions, including the timing and duration of dry periods¹⁴, control TPL deposition and
148 retention, with wide channels receiving proportionally less riparian material than narrow
149 ones¹⁹. TPL decomposability is typically altered during dry phases, due to partial degradation
150 or leaching of labile constituents during rainfall events, relative accumulation of recalcitrant
151 compounds, and leaching of labile constituents, relative accumulation of recalcitrant
152 compounds, and impoverishment of nutrients in terrestrial conditions^{15,20}. Therefore, we
153 predict that TPL accumulation and decomposability would be a function of climate, riparian

154 vegetation, channel topography, and duration of the dry phase (**Fig. 1**). We explored these
155 relationships by assessing the quantity and decomposability of accumulated TPL in 212 dry
156 river channels located in 22 countries distributed across wide environmental gradients and
157 multiple climate zones⁸ (**Supplementary Material 2**).

158

159 **Terrestrial plant litter accumulation in dry riverbeds**

160 Our results refine current understanding of the global distribution and variability in TPL
161 accumulation in IRES during dry phases. The quantity of TPL collected in 212 dry riverbeds
162 (**Supplementary Material 2**) ranged from 0 to 8291 g dry mass m⁻² (mean ± S.D. = 277 ±
163 796, median = 102 g m⁻²; **Table 1**). This material mainly comprised leaf litter (LL) and wood
164 (41% and 39% of the total mass, respectively), whereas herbs, fruits and catkins accounted for
165 <20% of the total mass (**Table 1**). The quantity of LL ranged from 0-963 g m⁻² (mean ± S.D.
166 = 88 ± 139, median = 36 g m⁻²).

167

168 Relationships between TPL quantity and environmental variables were assessed using
169 Random Forest models (RF), which are highly flexible regression techniques suitable for
170 modelling responses that show complex relationships with environmental conditions (e.g.,
171 climate, riparian zone, flow regime, channel topography). RF based on data from all samples
172 explained 41.4% and 38.3% of the total variance in TPL and LL quantity, respectively (**Table**
173 **2, Fig. 2**). Supporting our conceptual model (**Fig. 1**), aridity, mean annual precipitation,
174 catchment area, and dry period duration were the most important predictors of TPL quantity
175 (**Table 2**). Aridity, river width, riparian cover, time since senescence, and dry period duration
176 were most influential to determine LL accumulation (**Table 2**). LL quantity generally
177 increased with riparian cover and decreased with river width (**Fig. 2**). Relationships with time
178 since senescence, aridity, and dry period duration were more complex. LL quantity decreased

179 as the aridity index increased to 250, increased sharply until it reached 650 and then plateaued
180 (**Fig. 2**). LL quantity also increased almost linearly as dry period duration increased to 200 d,
181 and then dropped sharply (**Fig. 2**). The quantity of LL fell for 320 days after estimated
182 senescence and then rose slightly (**Fig. 2**).

183 The greatest quantity of terrestrial material, in particular LL, was reported from first-order,
184 forested, temperate IRES, suggesting these sites are hotspots of organic matter accumulation
185 in dendritic river networks. This finding concurs with patterns predicted by the River
186 Continuum Concept (RCC)²¹ but differ from its predictions regarding the fate of TPL entering
187 river channels. According to the RCC, a large portion of TPL entering forested headwaters is
188 immediately processed by heterotrophic microbes and invertebrate shredders, generating
189 significant amounts of fine-particulate organic matter that is exported downstream. In
190 contrast, we found TPL accumulations in dry channels to be greatly increased compared to
191 perennial rivers^{8,14}, because the absence of flowing water limits biological activity and
192 physical abrasion. During the initial phases when flow resumes, much of this material can
193 then be transported and further processed downstream^{9,10,16}.

194
195 Overall, LL accumulation in IRES matches global patterns in terrestrial inputs^{1,20}, revealing
196 strong biogeochemical and ecological links between rivers and adjacent terrestrial
197 ecosystems. The positive relationship between the degree of aridity and the quantity of
198 accumulated LL probably reflects water-limited riparian plant growth²², while the saturating
199 relationship observed above an index value of 700 suggest that, in humid conditions, LL
200 accumulation becomes limited by other factors. LL quantities in dry channels reflect a balance
201 between riparian and upstream inputs, and losses due to dry-phase decomposition and
202 downstream export during phases of flow. Downstream effects of LL transport and processing

203 when flow resumes will also depend on the decomposability of the accumulated organic
204 matter.

205

206 **Decomposability of accumulated leaf litter**

207 The mass C:N ratio of LL, as a first proxy of decomposability, ranged from 17 to 154 (mean \pm
208 S.D. = 46 ± 23) and was driven by climate, riparian cover, and dry period duration, as
209 predicted by our conceptual model (**Fig. 1**). However, the RF model explained only 14.9% of
210 the total variance in C:N (**Table 2**). The relationship of the C:N ratio with mean annual
211 potential evapotranspiration (PET) was not monotonic in that the C:N ratio increased sharply
212 between about 700 and 900 mm PET year⁻¹ and then gradually decreased (**Supplementary**
213 **Material 3**). The C:N ratio decreased with riparian cover and the aridity index, the latter
214 relationship resembling the reverse of its response to dry period duration (**Supplementary**
215 **Material 3**). Aridity was an important influence on C:N, with lower ratios reported for low-
216 aridity environments, including tropical conditions, compared to other climate types^{20,23}.
217 More research is needed to determine how plant species richness, vegetation structure and
218 functional diversity in riparian zones affect the C:N and decomposability of LL in dry
219 riverbeds.

220

221 Decomposability was also related to preconditioning after LL deposition on dry riverbeds. A
222 few days of drying on the riverbed decreased the C:N ratio of LL, whereas longer drying
223 periods resulted in increases, with peaks occurring after ~100 days before C:N declined again,
224 levelling off after 200 days (**Supplementary Material 3**). The increase in C:N with dry
225 period duration suggests that nutrients, along with other soluble compounds, are preferentially
226 leached from LL in dry riverbeds, resulting in litter composed mostly of nutrient-poor
227 structural compounds such as cellulose and lignin²⁴. The initial decomposability of LL falling

228 onto dry riverbeds and subsequent quality changes affect decomposition in both the receiving
229 and downstream reaches¹⁶. Thus, climate change-related extensions of dry periods¹³ could
230 increase downstream transport of low-quality LL, with potential repercussions on detrital food
231 webs and associated ecosystem functions and services.

232

233 **Respiration and CO₂ release after leaf litter rewetting**

234 We did not determine decomposition rates directly, but used a proxy of terrestrial litter
235 decomposability by measuring oxygen consumption related to rewetting in laboratory
236 conditions. Oxygen consumption rates of rewetted LL ranged from 0.004 to 0.97 mg O₂ g⁻¹
237 dry mass h⁻¹ (mean \pm S.D. = 0.36 \pm 0.20, median = 0.29). These values are in the upper range
238 of respiration rates reported from coarse-particulate organic matter in fresh waters and soils
239 (0.009-0.55 and <0.001–0.35 mg O₂ g⁻¹ dry mass h⁻¹ for fresh waters and soils, respectively;

240 **Supplementary Material 4**). This indicates that rewetting events are associated with intense
241 biological activity, when the highly labile C fuelling the initial respiration after rewetting can
242 be rapidly metabolised by most heterotrophic microorganisms present in the litter¹⁴. The
243 global RF model explained 36.8% of the total variation in O₂ consumption rates, with the
244 most important predictors being the riparian forest proportion in the catchment, catchment
245 area, the time since senescence, dry period duration, aridity, and the C:N ratio (**Table 2**,
246 **Supplementary Material 5**). Rates increased with catchment area, and decreased with forest
247 proportion, aridity, C:N, time since senescence, and dry period duration. Upon flow
248 resumption, higher microbial respiration rates are triggered when previous drying events are
249 short compared to extended dry phases. The predicted increase in the frequency of drying
250 events^{9,13} might have strong implications on IRES metabolism and thus increase their
251 contribution to the global C cycle through CO₂ emissions upon rewetting.

252

253 Our estimates of CO₂ emissions from IRES upon LL rewetting ranged from 0 to 13.7 g CO₂
254 m⁻² day⁻¹ (mean ± S.D. = 0.88 ± 1.51, median = 0.42), which is in the upper range of
255 previously reported daily emission rates from fresh waters and soils (**Supplementary**
256 **Material 6**). Notably, the highest daily values are 10-fold higher than those reported in the
257 most comprehensive estimates of CO₂ emission rates available from inland waters³, in which
258 reservoirs are expected to release up to 0.34 g CO₂ m⁻² day⁻¹ and perennial streams up to 1.75
259 g CO₂ m⁻² day⁻¹. Our highest potential CO₂ emission rate associated with LL rewetting could
260 thus represent up to 152% of previous estimates from perennial streams and rivers when
261 comparing daily emission rates (min = 0%, mean = 3-10%, max = 47-152%; **Supplementary**
262 **Material 7a**). This is remarkable, especially since our estimates are conservative, because
263 they are mainly based on microbial activity on LL and exclude sediment respiration. The
264 highest emission rates were found at sites characterised neither by the highest O₂ consumption
265 rates nor by the highest quantities of accumulated LL, indicating that the two variables are
266 uncorrelated. This highlights the need to consider both LL quantity and decomposability, to
267 evaluate the role of IRES in the global C cycle.

268

269 The RF model explained 34.9% of the total variation in the potential CO₂ released with
270 estimated time since senescence, aridity, and drying duration as the most important predictors
271 (**Table 2, Fig. 3a**). Relationships were typically non-monotonic. The CO₂ released decreased
272 sharply until 85 days after estimated senescence, before remaining relatively low and stable
273 (**Fig. 3a**). CO₂ release decreased till an aridity index value of 230, then increased sharply till
274 700 to decrease again and stabilise at values above 800 (**Fig. 3a**). Last, rates of CO₂ release
275 remained stable for 200 d of dry riverbeds, but sharply decreased thereafter (**Fig. 3a**).

276 Although IRES release CO₂ during both flowing^{3,25} and dry²⁶ phases, our study suggests that
277 early stages of rewetting can be considered hot moments^{9,11} or control points²⁷ of CO₂ release.

278 This finding is important because global estimates of CO₂ release focusing on perennial
279 rivers^{3,4,7,25} have missed emissions from at least 84,000 km² of river channel areas
280 (representing ~12.3% of total river and stream areas) by overlooking IRES^{3,28}.

281

282 **Differences among climate zones**

283 Our global study demonstrates that the quantities of organic material accumulating during dry
284 phases in riverbeds vary substantially among climate zones. Temperate IRES accumulated
285 more LL (mean \pm S.D. = 97 ± 152 , median = 41 g dry mass m⁻²) than those in the tropics
286 (mean \pm S.D. = 32 ± 44 , median = 9 g dry mass m⁻²) and arid climates (mean \pm S.D. = $45 \pm$
287 64 , median = 7 g dry mass m⁻²) (ANOVA, $P < 0.001$). Of the sampled riverbeds, 150, 31, 19,
288 and 10 were located in temperate, arid, tropical and continental climates, respectively,
289 reflecting the geographical spread of current IRES research²⁹ and highlighting that our results
290 need to be interpreted with caution in less well-represented climate classes, particularly in
291 alpine (only a single location), continental and, to a lesser extent, tropical IRES. When run
292 separately for different climate zones, RF model performance to predict the quantity of
293 accumulated LL was indeed much higher for temperate and arid (36.1% and 26.8% of total
294 variance explained, respectively) than for tropical (5.6%) climates. Thus, our conclusions are
295 more solid in temperate and arid climates, where IRES are widespread, compared to the
296 tropics^{30,31}. For example, IRES represent up to 45% of the hydrological network in temperate
297 France³² and up to 96% in the arid south-western USA^{33, 34}. Tropical IRES often have higher
298 annual LL inputs than temperate forests³⁵, but our ability to predict their LL accumulation in
299 these riverbeds was reduced, probably because of often continuous leaf fall³⁶. This result
300 might indicate that C cycling in IRES is less punctuated in tropical than in other climates,
301 although identical predictors were retained by the respective RF models, indicating that litter
302 accumulation is controlled by common factors across all climatic zones.

303

304 Our findings on LL accumulation were paralleled by estimates of CO₂ release upon rewetting,
305 which were also much higher in temperate (mean \pm S.D. = 1.06 ± 1.76 g CO₂ m⁻²) than in arid
306 and tropical IRES (0.48 ± 0.68 and 0.28 ± 0.35 g CO₂ m⁻², respectively). However, this
307 comparison is influenced by the limited ability of our models to predict CO₂ release from arid
308 IRES (4.4% of the variance explained) compared to temperate and tropical IRES (33.5 and
309 16.8% of the variance explained, respectively). This may reflect the role of abiotic processes
310 such as photodegradation for LL decomposition in water-limited river ecosystems¹⁵ or the
311 influence of plant functional traits, not included in our model, that are involved in the
312 protection from desiccation and solar radiation, such as the quantities of waxes and phenolic
313 compounds³⁷.

314

315 **Implications and perspectives**

316 Our global study spanning 212 reaches on all continents (i) enabled us to document the extent
317 of global variation in TPL and LL quantity and quality across dry riverbeds, and (ii) revealed
318 high O₂ consumption and CO₂ release rates after LL rewetting, notably in temperate regions.
319 These findings support the notion of IRES as punctuated biogeochemical reactors⁹,
320 characterised by distinct phases of C accumulation and processing with much higher temporal
321 variability in process rates than in perennial river ecosystems. Transport distance and site of
322 litter deposition and processing after flow resumes will vary with river morphology and the
323 magnitude of the flow pulse¹⁶. However, except during extreme flow conditions, much of the
324 mobilised litter will remain in river channels and riparian areas, where it decomposes at rates
325 similar to those in perennial rivers. Since these rates are much faster than in upland terrestrial
326 sites^{1,14}, these findings suggest that neglecting IRES leads to a notable underestimation of the
327 contribution of the world's river network to the total global CO₂ flux to the atmosphere. Our

328 study suggests that in addition to globally relevant amounts of CO₂ released from IRES
329 during both dry²⁶ (**Supplementary Material 7b**) and flowing phases, rewetting events act as
330 control points²⁷. This would imply upward revision of organic matter transformations and
331 CO₂ emissions from river networks on the global scale. Indeed, based on the comparison of
332 daily CO₂ emission rates with those reported from perennial rivers and streams, IRES could
333 increase estimates of global CO₂ emissions from streams and rivers by 7-152%, the CO₂
334 released from LL during a single rewetting event alone contributing roughly from 3 to 10% of
335 this increase (**Supplementary Material 7a**). Likewise, taking IRES into account would
336 improve estimates of the consequences of global climate change on C cycling, given that the
337 spatial extent of IRES will increase, and period of drying will become more prolonged, in
338 many regions^{9,11,13}.

339

340 The data and conceptual framework presented here provide the basis needed to develop
341 models of litter decomposition and C cycling in fresh waters that include IRES. The next
342 steps would be to quantify CO₂ emissions upon flow resumption *in situ*¹⁶ and collect data on
343 LL quantity and decomposability for continental and other climates that are not well
344 represented at present. CO₂ emissions from dry phases, suggested recently to be substantial²⁶,
345 along with those from flowing phases³, need to be integrated with those during wetting
346 events, and temporal variability (including its dependency on other environmental conditions,
347 such as temperature) be studied for extended periods after flow resumes to build adequate
348 quantitative models of global C cycling that consider the spatio-temporal dynamics of IRES
349 under present and future climatic conditions.

350

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- 422

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428

429 **Author contributions**

430 T. Datry, A. Foulquier, R. Corti, D. von Schiller, and K. Tockner assumed responsibility for
431 the overall project planning and coordination. All authors collected plant litter in their
432 countries and processed and analysed this material. The centralised lab analyses were
433 conducted by T. Datry, A. Foulquier, R.Corti, C. Mendoza–Lera, and J.C. Clement. The data
434 compilation and database management was carried out by R. Corti and C. Mendoza-Lera. The
435 data analyses were performed by T. Datry, R.Corti, A. Foulquier, and C. Mendoza–Lera. T.
436 Datry led the writing of the manuscript with A. Foulquier and notable contributions by M.O.
437 Gessner, B. Gücker, M. Moléon and R. Stubbington. All other authors commented on and
438 contributed to revising draft versions.

439

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442

443 **Competing interests**

444 The authors declare no competing financial or non-financial interests.

445

446 **Table and Figure captions**

447

448 **Table 1: Quantity (g dry mass.m⁻²) of terrestrial plant litter collected in dry riverbeds**
449 **(Min: minimum, Max: maximum, Mean, S.D.: standard deviation, Fraction: % of the**
450 **total quantity.**

451

452 **Table 2. Detailed results of global Random Forest (RF) models on five response**
453 **variables. The variables used as predictors are described in Supplementary Material 8.**
454 **INC MSE corresponds to the increase in the mean squared error of the predictions after**
455 **permutation. INC Node Purity is the average decrease in node impurity measured as**
456 **residual sum of squares. Both are used to assess the importance of predictors in an RF**
457 **model. The higher the value of both measures, the more important the variable.**

458

459 **Figure 1. Main variables predicted to control plant litter accumulation and**
460 **decomposability in intermittent rivers and ephemeral streams.** The accumulation of
461 terrestrial plant material is a function of the input of litter from riparian vegetation mediated
462 by its retention that depends on channel topography and the duration of dry events. Channel
463 topography and composition of the riparian vegetation are driven by flow regimes and,
464 ultimately, climate. Climate also influences the condition of the litter accumulated during dry

465 phases and hence its preconditioning. Photo credits: D. von Schiller (left panel) and M.
466 Moléon (right panel).

467

468 **Figure 2. Partial dependence of the probability of the quantity of leaf litter (LL)**
469 **accumulated in dry reaches.** Variables are shown from the top left to the bottom right in
470 order of decreasing importance. The plots show the marginal contribution to probability of the
471 quantity of LL accumulated in dry reaches (marginal response, y-axis) as a function of the
472 predictors (i.e. when the other contributing predictors are held at their mean). The rug plots on
473 the horizontal axes show deciles of the predictors.

474

475 **Figure 3. a. Partial dependence of the probability of the CO₂ released by rewetted leaf**
476 **litter (LL) over 24 h.** Variables are shown from left to right in order of decreasing
477 importance. The plots show the marginal contribution to probability of the CO₂ released by
478 rewetted LL over 24 h (marginal response, y-axis) as a function of the predictors (i.e. when
479 the other contributing predictors are held at their mean). The rug plots on the horizontal axes
480 show deciles of the predictors. **b. potential CO₂ released mapped onto the original**
481 **sampling reaches.**

482

483 **Methods**

484 **Sampling design.** Terrestrial plant litter (TPL) deposited on dry riverbeds was collected by
485 participants of an international consortium (http://1000_intermittent_rivers_project.irstea.fr⁸)
486 following a standardised protocol. In total, 212 near-natural river reaches were studied in 22
487 countries spanning 13 Köppen-Geiger climate classes (**Supplementary Material 2**). Briefly,
488 the sampled river reaches were 10 × the average active channel widths to cover a
489 representative area of each river channel and to ensure consistent sampling effort across
490 reaches³⁸. The active channel was defined as the area of frequently inundated and exposed

491 riverbed sediments between established edges of perennial, terrestrial vegetation and/or abrupt
492 changes in slope³⁹. TPL was collected by hand from 1 m² quadrats placed randomly within
493 each reach during a dry phase. The quadrats covered ~5% of the reach surface area (e.g. five
494 quadrats in a 100 m² reach). Different types of TPL (i.e. leaves, wood, fruits, catkins, herbs)
495 were stored in separate airtight plastic bags.

496

497 **Environmental variables.** A set of 22 environmental variables reflecting reach
498 characteristics at different spatial scales was estimated or calculated for each site
499 (**Supplementary Material 8**). Seventeen variables were determined locally. Mean annual
500 temperature and precipitation were extracted from the WorldClim.org database, which gives
501 1-km spatial resolution climate surfaces for global land areas over the period 1970-2000.
502 Mean annual potential evapotranspiration (PET) and mean annual aridity were determined
503 using the Global Aridity and PET database published by the Consortium for Spatial
504 Information (CGIARCSI, <http://www.cgiar-csi.org>) using the WorldClim.org database. PET
505 is a measure of the ability of the atmosphere to remove water through evapotranspiration and
506 was calculated as a function of annual mean temperature, daily temperature range and extra-
507 terrestrial radiation between 1950 and 2000. Mean annual aridity was assessed using an
508 aridity index⁴⁰ and expressed as $1\,000 \times \text{precipitation} / \text{PET}$ between 1950 and 2000. Aridity
509 index values were high in humid and low in arid conditions. Climate zones following the
510 Köppen-Geiger system were determined from the global climate map derived from long-term
511 monthly precipitation and temperature time series in a grid of weather stations and
512 interpolated among stations using a two-dimensional (latitude and longitude) thin-plate spline
513 with tension onto a 0.1° by 0.1° grid for each continent⁴¹. Last, we estimated time since leaf
514 abscission as the time between the estimated onset of leaf senescence and the sampling date.
515 Although leaf fall is more continuous in tropical areas than in other climate zones, to facilitate

516 comparison among sites, onset of leaf senescence was set to the 1st of September and the 15th
517 of February in the northern and southern hemispheres, respectively⁴².

518

519 **Litter drying, weighing and grinding.** TPL was transported to local laboratories within 8 h
520 of collection when possible and oven dried at 60 °C for ≥ 12 h (<24 h for leaves). Fresh
521 material such as fruits or wood was dried at room temperature for 1 week before oven drying.
522 The dried material was weighed to the nearest gram. Although wood can account for
523 considerable volumes of TPL deposited in riverbeds, it is far more recalcitrant than leaf litter
524 (LL). Therefore, we focused on LL in our assessment of TPL decomposability during short-
525 term rewetting events. LL was thoroughly mixed before taking a 60-g subsample that was first
526 shredded by hand and passed through a 0.5-cm mesh screen, then shipped to the IRSTEA
527 laboratory (Lyon, France) for further processing.

528

529 **Decomposability of leaf litter.** Laboratory measurements can provide a useful means to
530 address global-scale environmental research questions⁴³ and overcome the current data
531 shortage on intermittent rivers and ephemeral streams. In particular, they facilitate tests of
532 between-reach variability in O₂ consumption rates in a standardised way and identification of
533 the primary drivers responsible for the observed variability. Although we did not quantify
534 decomposition rates directly, we assessed two proxies of LL decomposability, the C:N mass
535 ratio and oxygen (O₂) consumption rate after rewetting.

536

537 Three 10-mg LL subsamples were taken from each sample, ground to 5 μ m with a ball mill
538 (MM301, Retsch GmbH, Haan, Germany) and the C:N ratio determined with an elemental
539 analyzer (FlashEA 1112, Fisher Scientific, Waltham, Massachusetts, USA). O₂ consumption
540 was determined in respiration flasks placed in a climatic room at 20 °C. LL subsamples were

541 processed in 10 successive batches of 25-50 subsamples. Each batch was incubated in three
542 200-L polyethylene containers filled with tap water at room temperature to prevent O₂
543 exchange with the atmosphere. For each subsample, two analytical replicates were processed
544 by placing 0.1 g LL into 250-mL glass respiration flasks filled with Volvic® mineral water,
545 then sealed airtight using a 3.2-mm-thick silicon-PTFE septum and a cut-out open-top cap.
546 Care was taken to ensure air bubbles were excluded. O₂ concentrations were measured with a
547 needle-based micro-optode (Oxygen Microsensor PM-PSt7; PreSens, Regensburg, Germany)
548 using a stand-alone, portable, fiber-optic O₂ meter (Microx 4 trace; PreSens, Regensburg,
549 Germany). Incubations were run for approximately 24 h (range of incubation times: 23.4-25.8
550 h; mean ± S.D. = 24.3 ± 2.0 h) to simulate short-term rewetting events. We used LL
551 communities as a source of microbes, because dry LL hosts dormant communities that can
552 quickly resume activity after litter rewetting⁴⁴. We also ran tests to ensure our oxygen
553 consumption rates were realistic. This was achieved by using LL, different sources of water
554 with and without a standard inoculum from local streams (see below).
555
556 O₂ concentrations were measured twice, 2 h and 24 h after the respiration flasks were filled
557 with water. We waited for 2 h before taking the first measurement to allow gas release from
558 air-saturated pores within the LL⁴⁵. Although the respiration flasks were carefully filled
559 without bubbling the water, we left them open for 2 h while the LL released gas, to ensure
560 that O₂ concentration was saturated, but not supersaturated to avoid a notable underestimation
561 of respiration rates over 24 h. Flasks were gently agitated every 6 h during the incubation
562 period and before each measurement to ensure homogenous O₂ concentrations in the water.
563 For each batch, O₂ concentrations were also measured in three control respiration flasks filled
564 with Volvic® mineral water only. Microbial respiration associated with LL (R: mg O₂ g⁻¹ LL
565 dry mass h⁻¹) was calculated as:

$$R = \frac{(O_{2sample}^{2h} - O_{2sample}^{24h}) - (O_{2control}^{2h} - O_{2control}^{24h})}{incubation\ time(h)} \times respiration\ flask\ volume$$

566

(g)

567 where O_2 is the dissolved O_2 concentration ($mg\ L^{-1}$); the subscripts sample and control refer to
 568 each analytical replicate and the mean O_2 of the three control respiration flasks; and the
 569 superscripts 2 h and 24 h correspond to the O_2 concentrations measured 2 h and 24 h after the
 570 flask was filled, respectively. R was then standardised to 20 °C to correct for small (i.e., \pm
 571 1.1 °C) temperature variations during the measurements, assuming that O_2 consumption rates
 572 double with a temperature increase of 10 °C⁴⁶. The mean of the two analytical replicates was
 573 used as a measure of microbial respiration associated with LL rewetting for each sample. For
 574 10 samples, we had not sufficient litter material to conduct the respiration measures and for
 575 another 6, the material was not adequately processed by the collectors and was thus excluded
 576 from the analysis. Hence, the total number of samples analysed for O_2 consumption rates was
 577 196 (**Supplementary Material 9**).

578

579 The total potential CO_2 released per m^2 of riverbed over 24 h after rewetting was estimated by
 580 multiplying, for each sampling site, the amount of accumulated LL (in g per m^2) by the rate of
 581 O_2 consumption ($mg\ O_2\ g^{-1}\ LL\ dry\ mass\ h^{-1}$) over 24h (**Supplementary Material 9**). The
 582 obtained estimates of O_2 consumption ($mg\ O_2\ m^{-2}\ day^{-1}$) were then converted into CO_2
 583 production ($mg\ CO_2\ m^{-2}\ day^{-1}$) by assuming a respiratory quotient of 1⁴⁷.

584

585 **Sensitivity of O_2 consumption measurements.** To explore the sensitivity of our laboratory
 586 protocol to assess LL respiration in the initial stage of rewetting, we compared O_2
 587 consumption rates with and without a microbial inoculum added (**Supplementary Material**
 588 **10**). The inoculum was prepared from sediments collected with a shovel from a flowing reach
 589 of the Albarine River close to Lyon, France¹⁴. We added 250 mL of Volvic® water to 250 mL

590 of sediment and placed it twice in an ultrasonic bath (Branson 5510E, Emerson, MO, USA)
591 for 30 s. The suspension of water and sediment was gently shaken after ultrasonication. We
592 then added 2.5 mL of the inoculum suspension to each respiration flask before filling them
593 with Volvic® water. Before adding the inoculum, the suspension was gently shaken again to
594 ensure a uniform inoculum distribution within the flask. In addition, we compared oxygen
595 consumption rates without inoculum by using stream water from three LL collection sites
596 (Albarine, Audeux and Calavon), instead of Volvic® mineral water (**Supplementary**
597 **Material 10**). We did not use an inoculum in our final experiments, because: a) it is
598 conceptually problematic to use an inoculum from one system to quantify the
599 decomposability of material from other areas and the large variability induced by doing so
600 could mask large-scale patterns of oxygen consumption rates upon rewetting; b) it was
601 impractical to ask international participants to send 2-3 L of river water to IRSTEA,
602 especially when the rivers were dry; c) it is virtually impossible to keep an inoculum constant
603 among runs in laboratory microcosms. By not adding an inoculum, our O₂ consumption rates
604 were likely underestimated (i.e. conservative) relative to in-situ rates of O₂ consumption
605 (**Supplementary Material 10**).

606

607 **Data analysis.** We used random forests (RFs) to explore relationships between environmental
608 variables and TPL quantity, LL decomposability, and CO₂ release upon rewetting events. RFs
609 are highly flexible regression techniques suitable for modelling response variables (e.g., the
610 quantity and decomposability of TPL) that show complex relationships with environmental
611 variables (e.g., climate, riparian zone, flow regime, channel topography). RFs are invariant to
612 monotonic transformations of environmental variables, perform better than other regression
613 techniques when facing multicollinearity, are relatively robust to over-fitting, automatically fit

614 non-linear relationships and high-order interactions, provide an overall goodness-of-fit
615 measure (R^2) and a measure of importance of each variable in a model⁴⁸⁻⁵⁰.

616

617 The role of environmental variables in RF models can be examined using importance
618 measures and partial dependence plots. Importance measures provide the contribution of
619 variables to model accuracy and are obtained from the degradation in model performance
620 when a predictor is randomly permuted^{48,50}. Partial dependence plots show the marginal
621 contribution of a variable to the response (i.e., the response as a function of the variable when
622 the other variables are held at their mean value⁴⁸⁻⁵⁰) and were used to interpret the
623 relationships between predictors and dependent variables (responses), which were $\log_{10}(x+1)$
624 transformed prior to analyses. Sets of global RF models were run for the main dependent
625 variables (quantities of TPL and LL; LL C:N, respiration rate and CO₂ production) and then
626 these RF sets were run for each of three climate zones, using the Köppen-Geiger classification
627 of sampling sites: arid (merging Köppen-Geiger BSh, BSk, BWh and BWk; n=31), temperate
628 (merging Cfa, Cfb, Csa, Csb, Cwa; n=150) and tropical (merging As, Aw; n=19). No RF
629 models were run for alpine and continental climates due to the low number (≤ 10) of sampling
630 sites.

631

632 We ran all global and climate-specific models with and without ‘time since senescence’ as a
633 predictor to assess the potential of this variable to improve predictive power, despite the large
634 uncertainty of this variable in some climate zones, particularly in the tropics. Removing the
635 variable from the models did not improve or diminish predictive power, including for IRES in
636 the tropics, but since RF models selected it as a strong predictor for most response variables,
637 we decided to include it in the analyses. The threshold to assess statistical significance was
638 0.05 for all analyses, which were conducted in R 3.3.3⁵¹ using the “RandomForest” package⁵².

639

640 **Data availability:** The presented data are available on the FIGSHARE repository under the

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642

643 **Code availability:** Not applicable.

644

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