nature geoscience

ARTICLES

https://doi.org/10.1038/s41561-018-0134-4

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

T. Datry[1,2*], A. Foulquier[3], R. Corti[1], D. von Schiller[4], K. Tockner[5,6], C. Mendoza-Lera[1], J. C. Clément[7], M. O. Gessner[5,8], M. Moleón[9], R. Stubbington[10], B. Gücker[11], R. Albariño[12], D. C. Allen[13], F. Altermatt[14], M. I. Arce[4], S. Arnon[15], D. Banas[16], A. Banegas-Medina[17], E. Beller[18], M. L. Blanchette[19], J. F. Blanco-Libreros[20], J. J. Blessing[21], I. G. Boëchat[22], K. S. Boersma[23], M. T. Bogan[24], N. Bonada[25], N. R. Bond[26], K. C. Brintrup Barría[27], A. Bruder[28], R. M. Burrows[29], T. Cancellario[30], C. Canhoto[31], S. M. Carlson[32], S. Cauvy-Fraunié[1], N. Cid[25], M. Danger[33], Bianca de Freitas Terra[34], A. M De Girolamo[35], Evans de La Barra[36], R. del Campo[37], V. D. Diaz-Villanueva[12], F. Dyer[38], A. Elosegi[4], E. Faye[39], C. Febria[40], B. Four[41], S. Gafny[42], S. D. Ghate[43], R. Gómez[37], L. Gómez-Gener[44], M. A. S. Graça[45], S. Guareschi[37], F. Hoppeler[46], J. L. Hwan[32], J. I. Jones[47], S. Kubheka[48], A. Laini[49], S. D. Langhans[5], C. Leigh[29], C. J. Little[50], S. Lorenz[51], J. C. Marshall[21], E. Martín[50], A. R. McIntosh[40], E. I. Meyer[52], M. Miliša[53], M. C. Mlambo[54], M. Morais[55], N. Moya[56], P. M. Negus[21], D. K. Niyogi[57], A. Papatheodoulou[58], I. Pardo[59], P. Pařil[60], S. U. Pauls[46], V. Pešić[61], M. Polášek[60], C. T. Robinson[50], P. Rodríguez-Lozano[32], R. J. Rolls[38], M. M. Sánchez-Montoya[37], A. Savić[62], O. Shumilova[5], K. R. Sridhar[43], A. L. Steward[21], R. Storey[63], A. Taleb[64], A. Uzan[65], Ross Vander Vorste[66], N. J. Waltham[67], C. Woelfle-Erskine[32], D. Zak[5,68], C. Zarfl[69] and A. Zoppini[35]

Perennial rivers and streams make a disproportionate contribution to global carbon (C) cycling. However, the contribution of intermittent rivers and ephemeral streams (IRES), which sometimes cease to flow and can dry completely, is largely ignored although they represent over half the global river network. Substantial amounts of terrestrial plant litter (TPL) accumulate in dry riverbeds and, upon rewetting, this material can undergo rapid microbial processing. We present the results of a global research collaboration that collected and analysed TPL from 212 dry riverbeds across major environmental gradients and climate zones. We assessed litter decomposability by quantifying the litter carbon-to-nitrogen ratio and oxygen (O_2) consumption in standardized assays and estimated the potential short-term CO_2 emissions during rewetting events. Aridity, cover of riparian vegetation, channel width and dry-phase duration explained most variability in the quantity and decomposability of plant litter in IRES. Our estimates indicate that a single pulse of CO_2 emission upon litter rewetting contributes up to 10% of the daily CO_2 emission from perennial rivers and stream, particularly in temperate climates. This indicates that the contributions of IRES should be included in global C-cycling assessments.

Decomposition of terrestrial plant litter (TPL) is an essential, biosphere-scale ecosystem process[1]. Of 120 Pg of organic carbon (C) produced by terrestrial plants annually, about half is respired by the plants but only a small fraction is removed by herbivores, so that up to 60 Pg enter the dead organic matter pool[1,2]. Fresh waters make a disproportionate contribution to global C cycling through TPL decomposition and atmospheric CO_2 emissions[3,4]. This contribution is particularly apparent in perennial rivers and streams, in which water and nutrient availability stimulate a rapid decomposition by microbes and invertebrate detritivores[1,3,5]. TPL deposited in fresh waters and the release of its decomposition products are critical energy sources that support food webs and ecosystem processes, which include key C-cycling pathways[1,5].

A major shortcoming of current estimates of the contribution of rivers and streams to global C cycling[3,6,7] is the omission of intermittent rivers and ephemeral streams (IRES), in which drying and rewetting events create ecosystems that transition between terrestrial and aquatic phases[8–10]. IRES are widespread ecosystems that drain a large proportion of the terrestrial biomes across all continents and climate types[9,11,12]. Moreover, IRES are increasing in extent due to global change[8,13]. During the dry phase, TPL deposited on the riverbed accumulates, decomposing only slowly through photodegradation and terrestrial decomposer activity[14,15]. Then, when flow resumes, the accumulated material is mobilized and transported downstream[16,17] (Supplementary Material 1). Concentrations of particulate and dissolved organic matter in advancing wetted fronts exceed the baseflow concentrations by several orders of magnitude[16]. Therefore, IRES have been conceptualized as punctuated biogeochemical reactors[9].

To understand the role of IRES in global C cycling, global-scale data are needed to characterize the variables that control TPL

A full list of authors and affiliations appears at the end of the paper.

accumulation in dry channels and its decomposability upon flow resumption. Climate influences the type and productivity of riparian vegetation[18] and the flow regimes of IRES[8,13]. Channel topography and flow conditions, which include the timing and duration of dry periods[14], control TPL deposition and retention, and wide channels receive proportionally less riparian material than narrow ones[19]. TPL decomposability is typically altered during dry phases due to the partial degradation or leaching of labile constituents during rainfall events, relative accumulation of recalcitrant compounds and leaching of labile constituents, relative accumulation of recalcitrant compounds and impoverishment of nutrients in terrestrial conditions[15,20]. Therefore, we predict that TPL accumulation and decomposability varies as a function of climate, riparian vegetation, channel topography and duration of the dry phase (Fig. 1). We tested these predictions by assessing the quantity and decomposability of accumulated TPL in 212 dry river channels located in 22 countries distributed across wide environmental gradients and multiple climate zones[8] (Supplementary Material 2).

TPL accumulation in dry riverbeds

Our results refine the current understanding of the global distribution and variability in TPL accumulation in IRES during dry phases. The quantity of TPL collected in 212 dry riverbeds (Supplementary Material 2) ranged from 0 to 8,291 g dry mass m^{-2} (mean $\pm$ s.d. = 277 $\pm$ 796, median = 102 g dry mass m^{-2} (Table 1)). This material mainly comprised leaf litter (LL) and wood (41% and 39% of the total mass, respectively), whereas herbs, fruits and catkins accounted for <20% of the total mass (Table 1). The quantity of LL ranged from 0 to 963 g dry mass m^{-2} (mean $\pm$ s.d. = 88 $\pm$ 139, median = 36 g dry mass m^{-2}).

Relationships between TPL quantity and environmental variables were assessed using random forest (RF) models, which are highly flexible regression techniques suitable for modelling responses that show complex relationships with environmental conditions (for example, climate, riparian zone, flow regime, channel topography). RF models based on data from all the samples explained 41.4% and 38.3% of the total variance in TPL and LL quantity, respectively (Fig. 2 and Table 2). Supporting our conceptual model (Fig. 1), aridity, mean annual precipitation, catchment area and dry-period duration were the most important predictors of TPL quantity (Table 2). Aridity, river width, riparian cover, time since senescence and dry-period duration were the most influential in determining LL accumulation (Table 2). LL quantity generally increased with riparian cover and decreased with river width (Fig. 2). Relationships with time since senescence, aridity and dry-period duration were more complex. LL quantity decreased as the aridity index increased to 250, increased sharply until it reached 650 and then plateaued (Fig. 2). LL quantity also increased almost linearly as the dry-period duration increased to 200 days, and then dropped sharply (Fig. 2). The quantity of LL fell for 320 days after the estimated senescence and then rose slightly (Fig. 2).

The greatest quantity of terrestrial material, in particular LL, was reported from first-order, forested, temperate IRES, which suggests that these sites are hotspots of organic matter accumulation in dendritic river networks. This finding concurs with patterns predicted by the river continuum concept (RCC)[21], but differ from its predictions with regard to the fate of TPL that enters river channels. According to the RCC, a large portion of TPL that enters forested headwaters is immediately processed by heterotrophic microbes and invertebrate shredders, which generates significant amounts of fine-particulate organic matter that is exported downstream. In contrast, we found TPL accumulations in dry channels to be greatly increased compared to those in perennial rivers[8,14], because the absence of flowing water limits the biological activity and physical abrasion. During the initial phases in which flow resumes, much of this material can then be transported and further processed downstream[9,10,16].

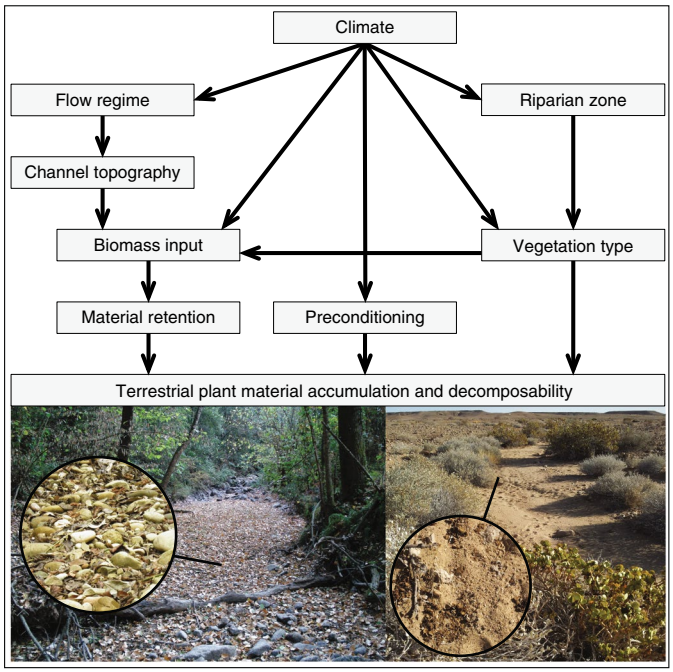

Fig. 1 | Main variables predicted to control plant litter accumulation and decomposability in IRES. The accumulation of terrestrial plant material is a function of the input of litter from riparian vegetation mediated by its retention, which depends on channel topography and the duration of dry events. Channel topography and composition of the riparian vegetation are driven by flow regimes and, ultimately, climate. Climate also influences the condition of the litter accumulated during dry phases and hence its preconditioning. Photo credits: D. von Schiller (left panel) and M. Moleón (right panel)

Overall, LL accumulation in IRES matches global patterns in terrestrial inputs[1,20], which reveals strong biogeochemical and ecological links between rivers and adjacent terrestrial ecosystems. The positive relationship between the degree of aridity and the quantity of accumulated LL probably reflects water-limited riparian plant growth[22], and the saturating relationship observed above an index value of 700 suggests that, in humid conditions, LL accumulation becomes limited by other factors. LL quantities in dry channels reflect a balance between riparian and upstream inputs and losses due to dry-phase decomposition and downstream export during phases of flow. The downstream effects of LL transport and processing when flow resumes also depend on the decomposability of the accumulated organic matter.

Decomposability of accumulated LL

The mass carbon-to-nitrogen (C:N) ratio of LL, as a first proxy of decomposability, ranged from 17 to 154 (mean $\pm$ s.d. = 46 $\pm$ 23) and was driven by climate, riparian cover and dry-period duration, as predicted by our conceptual model (Fig. 1). However, the RF model explained only 14.9% of the total variance in C:N (Table 2). The relationship of the C:N ratio with mean annual potential evapotranspiration (PET) was not monotonic in that the C:N ratio increased sharply between about 700 and 900 mm PET yr^{-1} and then gradually decreased (Supplementary Material 3). The C:N ratio decreased with riparian cover and the aridity index, and the latter relationship resembled the reverse of its response to dry-period duration (Supplementary Material 3). Aridity was an important influence on C:N, with lower ratios reported for low-aridity environments, which include tropical conditions compared to other climate types[20,23]. More research is needed to determine how plant-species richness,

Table 1 | Quantity of TPL collected in dry riverbeds

Type of material	Minimum (g dry mass m^{-2})	Maximum (g dry mass m^{-2})	Mean	s.d.	Fraction (%)
TPL	0	8,291	277	796	100
LL	0	963	88	139	41
Wood	0	7,812	154	715	39
Herbs	0	500	9	40	7
Fruits	0	351	12	42	4
Catkins	0	41	1	4	1
Miscellaneous	0	561	17	58	8

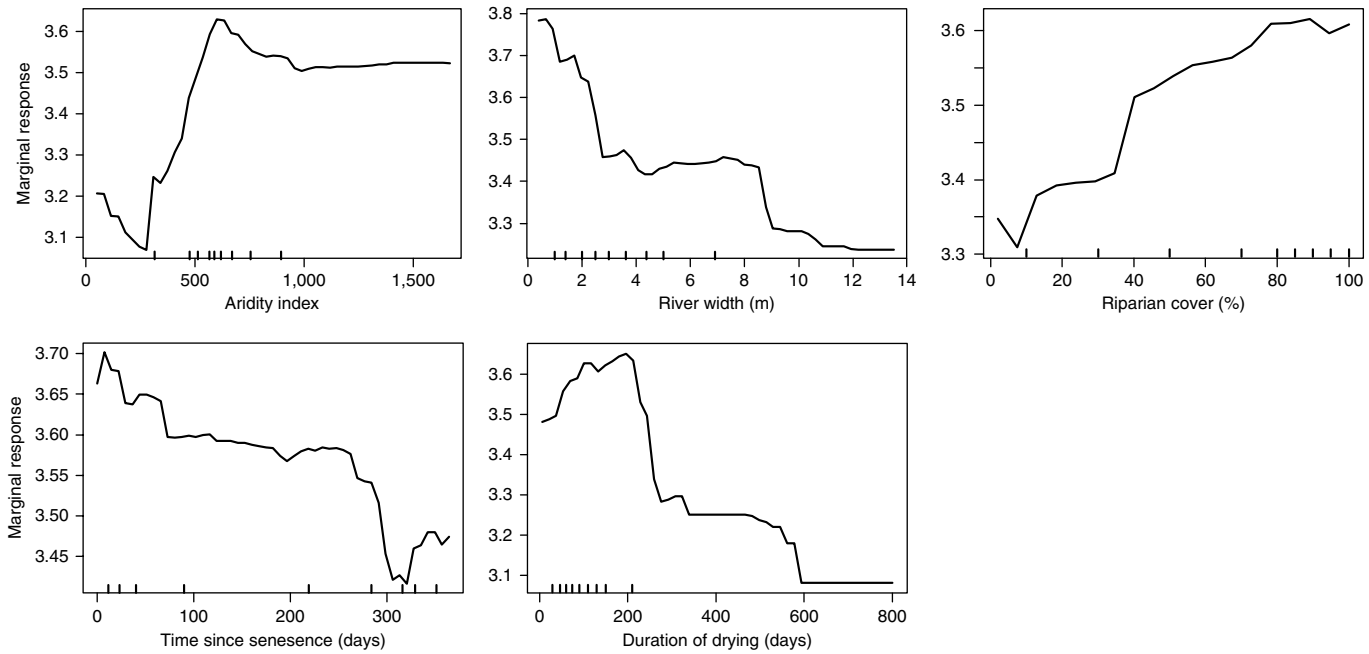

Fig. 2 | Partial dependence of the probability of the quantity of LL accumulated in dry reaches. Variables are shown from the top left to the bottom right in the order of decreasing importance. The plots show the marginal contribution to the probability of the quantity of LL accumulated in dry reaches as a function of the predictors (that is, when the other contributing predictors are held at their mean). The rug plots on the horizontal axes show deciles of the predictors.

vegetation structure and functional diversity in riparian zones affect the C:N and decomposability of LL in dry riverbeds.

Decomposability was also related to the preconditioning after LL deposition on dry riverbeds. A few days of drying on the riverbed decreased the C:N ratio of LL, whereas longer drying periods resulted in increases, with peaks occurring occurred after ~100 days before the C:N declined again and levelled off after 200 days (Supplementary Material 3). The increase in C:N with dry-period duration suggests that nutrients, along with other soluble compounds, are preferentially leached from LL in dry riverbeds, which results in litter composed mostly of nutrient-poor structural compounds, such as cellulose and lignin[24]. The initial decomposability of LL that falls onto dry riverbeds and subsequent quality changes affect the decomposition in both the receiving and downstream reaches[16]. Thus, extensions of dry periods related to climate change[13] could increase downstream transport of low-quality LL, with potential repercussions on detrital food webs and associated ecosystem functions and services.

Respiration and CO_2 release after LL rewetting

We did not determine decomposition rates directly, but used a proxy of terrestrial litter decomposability by measuring oxygen consumption related to rewetting in laboratory conditions. Oxygen consumption rates of rewetted LL ranged from 0.004 to 0.97 mg O_2 g^{-1} dry mass h^{-1} (mean ± s.d. = 0.36 ± 0.20, median = 0.29). These values are in the upper range of respiration rates reported from coarse particulate organic matter in fresh waters and soils (0.009–0.55 and <0.001–0.35 mg O_2 g^{-1} dry mass h^{-1} for fresh waters and soils, respectively (Supplementary Material 4). This indicates that rewetting events are associated with intense biological activity when the highly labile C fuelling the initial respiration after rewetting can be rapidly metabolized by most heterotrophic microorganisms present in the litter[14]. The global RF model explained 36.8% of the total variation in O_2 consumption rates, with the most important predictors being the riparian forest proportion in the catchment, catchment area, the time since senescence, dry-period duration, aridity and the C:N ratio (Table 2 and Supplementary Material 5). Rates increased with catchment area, and decreased with forest proportion, aridity, C:N, time since senescence and dry-period duration. Upon flow resumption, higher microbial respiration rates are triggered when previous drying events are short compared to extended dry phases. The predicted increase in the frequency of drying events[9,13] might have strong implications on IRES metabolism and thus increase their contribution to the global C cycle through CO_2 emissions upon rewetting.

Our estimates of CO_2 emissions from IRES upon LL rewetting ranged from 0 to 13.7 g CO_2 m^{-2} day^{-1} (mean ± s.d. = 0.88 ± 1.51,

Table 2 | Detailed results of global RF models on five response variables

Response variable	Variance explained (%)	Variable	Inc. MSE (%)	Inc. node purity
Total TPL	41.4	Aridity	31.9	34.9
		Rain	29.1	36.4
		Catchment area	25.3	34.2
		Duration of dry period	19.6	25.7
LL	38.3	Aridity	47.4	23.8
		River channel width	40.8	26.7
		Riparian cover	37.2	23.8
		Time since senescence	30.6	19.1
		Duration of dry period	30.3	26.5
C:N	14.9	PET	63.5	2.9
		Duration of dry period	48.3	2.1
		Riparian cover	47.6	2.1
		Aridity	42.2	2.0
Respiration rate	36.8	Riparian forest	68.6	0.3
		Catchment area	60.5	0.2
		Time since senescence	51.7	0.2
		Duration of dry period	48.2	0.2
		Aridity	38.7	0.1
		C:N	35.2	0.1
CO_2 release	31.9	Time since senescence	57.7	38.3
		Aridity	49.7	27.3
		Duration of dry period	44.1	36.7

The variables used as predictors are described in Supplementary Material 8. Inc. MSE corresponds to the increase in the mean squared error of the predictions after permutation. Inc. node purity is the average decrease in node impurity measured as the residual sum of squares. Both are used to assess the importance of predictors in an RF model. The higher the value of both measures, the more important the variable.

median = 0.42), which is in the upper range of previously reported daily emission rates from fresh waters and soils (Supplementary Material 6). Notably, the highest daily values are tenfold higher than those reported in the most comprehensive estimates of CO_2 emission rates available from inland waters[3], in which reservoirs are expected to release up to 0.34 g CO_2 m^{-2} day^{-1} and perennial streams up to 1.75 g CO_2 m^{-2} day^{-1}. Our highest potential CO_2 emission rate associated with LL rewetting could thus represent up to 152% of previous estimates from perennial streams and rivers when comparing daily emission rates (minimum = 0%, mean = 3–10%, maximum = 47–152% (Supplementary Material 7a)). This is remarkable, especially as our estimates are conservative because they are mainly based on microbial activity on LL and exclude sediment respiration. The highest emission rates were found at sites characterized neither by the highest O_2 consumption rates nor by the highest quantities of accumulated LL, which indicates that the two variables are uncorrelated. This highlights the need to consider both LL quantity and decomposability to evaluate the role of IRES in the global C cycle.

The RF model explained 34.9% of the total variation in the potential CO_2 released with estimated time since senescence, aridity and drying duration as the most important predictors (Fig. 3a and Table 2). Relationships were typically non-monotonic. The CO_2 released decreased sharply until 85 days after the estimated senescence, before it remained relatively low and stable (Fig. 3a). CO_2 release decreased until an aridity index value of 230, then increased sharply to 700 and then decreased again and stabilized at values above 800 (Fig. 3a). Last, rates of CO_2 release remained stable for 200 days of dry riverbeds, but sharply decreased thereafter (Fig. 3a). Although IRES release CO_2 during both the flowing[3,25] and dry[26] phases, our study suggests that the early stages of rewetting can be considered hot moments[9,11] or control points[27] of CO_2 release. This finding is important because global estimates of CO_2 release that focus on perennial rivers[3,4,7,25] have missed emissions from at least 84,000 km^2 of river channel areas (which represents ~12.3% of the total river and stream areas) by overlooking IRES[3,28].

Differences among climate zones

Our global study demonstrates that the quantities of organic material that accumulate during dry phases in riverbeds vary substantially among climate zones. Temperate IRES accumulated more LL (mean ± s.d. = 97 ± 152, median = 41 g dry mass m^{-2}) than those in the tropics (mean ± s.d. = 32 ± 44, median = 9 g dry mass m^{-2}) and arid climates (mean ± s.d. = 45 ± 64, median = 7 g dry mass m^{-2}) (analysis of variance, $P < 0.001$). Of the sampled riverbeds, 150, 31, 19 and 10 were located in temperate, arid, tropical and continental climates, respectively, which reflects the geographical spread of current IRES research[29] and highlights that our results need to be interpreted with caution in less well-represented climate classes, particularly in alpine (only a single location), continental and, to a lesser extent, tropical IRES. When run separately for different climate zones, RF model performance to predict the quantity of accumulated LL was, indeed, much higher for temperate and arid (36.1% and 26.8% of the total variance explained, respectively) than for tropical (5.6%) climates. Thus, our conclusions are more solid in temperate and arid climates, where IRES are widespread, compared to those for the tropics[30,31]. For example, IRES represent up to 45% of the hydrological network in temperate France[32] and up to 96% in the arid southwestern United States[33,34]. Tropical IRES often have higher annual LL inputs than those of temperate forests[35], but our ability to predict the LL accumulation in these riverbeds was reduced, probably because of the often continuous leaf fall[36]. This result might indicate that C cycling in IRES is less punctuated in tropical than in other climates, although identical predictors were retained by the respective RF models, which indicates that litter accumulation is controlled by common factors across all climatic zones.

Our findings on LL accumulation were parallelled by estimates of CO_2 release upon rewetting, which were also much higher in temperate (mean ± S.D. = 1.06 ± 1.76 g CO_2 m^{-2}) than in arid and tropical IRES (0.48 ± 0.68 and 0.28 ± 0.35 g CO_2 m^{-2}, respectively). However, this comparison is influenced by the limited ability of our models to predict CO_2 release from arid IRES (4.4% of the variance explained) compared to temperate and tropical IRES (33.5 and 16.8% of the variance explained, respectively). This may reflect the role of abiotic processes, such as photodegradation for LL decomposition in water-limited river ecosystems[15] or the influence of plant functional traits, not included in our model but that are involved in the protection from desiccation and solar radiation, such as the quantities of waxes and phenolic compounds[37].

Implications and perspectives

Our global study spanned 212 river reaches on all continents and (1) enabled us to document the extent of global variation in TPL and LL quantity and quality across dry riverbeds and (2) revealed

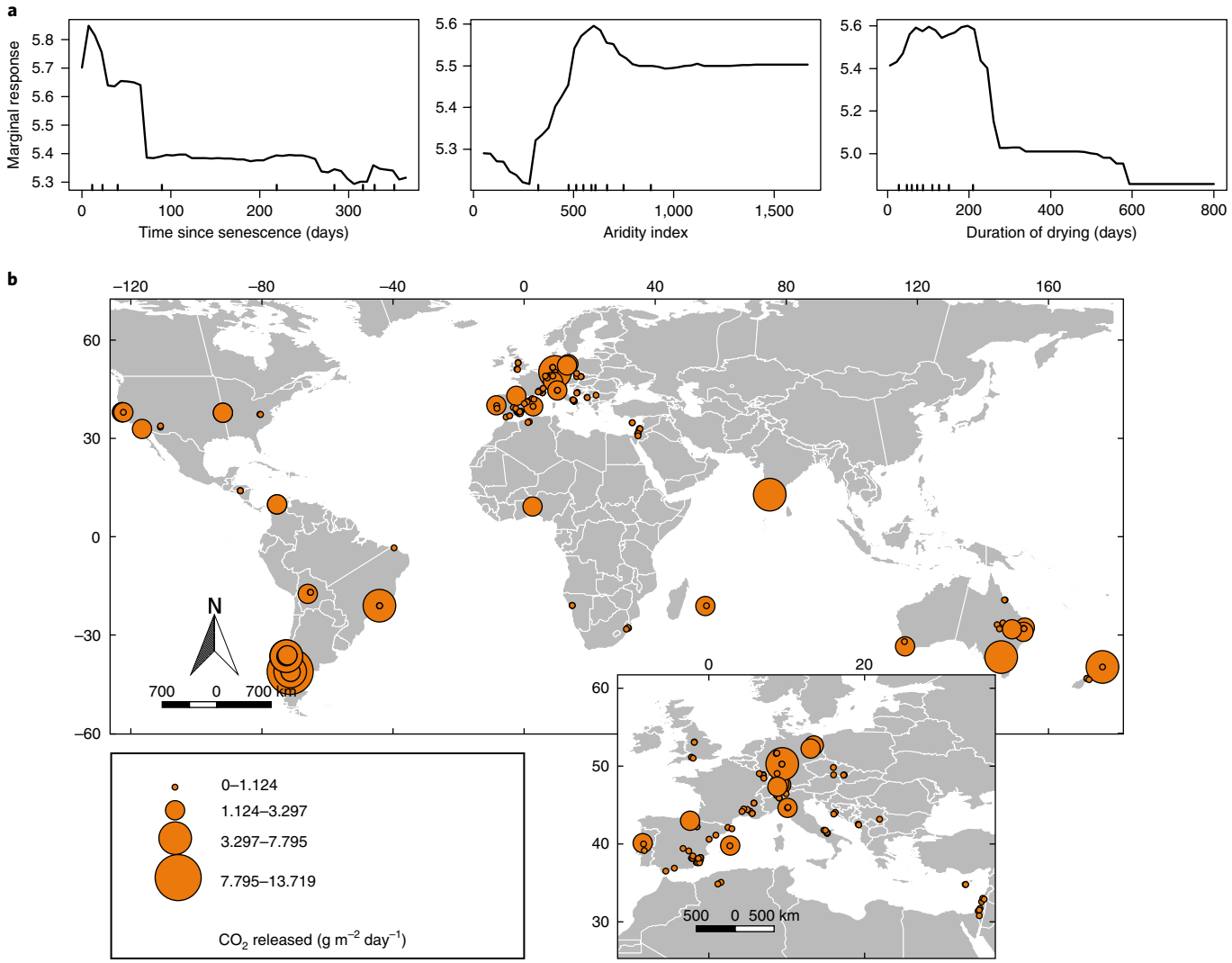

Fig. 3 | CO_2release. a, Partial dependence of the probability of the CO_2 released by rewetted LL over 24 h. Variables are shown from left to right in order of decreasing importance. The plots show the marginal contribution to the probability of the CO_2 released by rewetted LL over 24 h as a function of the predictors (that is, when the other contributing predictors are held at their mean). The rug plots on the horizontal axes show deciles of the predictors. **b**, Potential CO_2 released mapped onto the original sampling reaches.

high O_2 consumption and CO_2 release rates after LL rewetting, notably in temperate regions. These findings support the notion of IRES as punctuated biogeochemical reactors[9] characterized by distinct phases of C accumulation and processing with much higher temporal variabilities in process rates than in perennial river ecosystems. The transport distance and site of litter deposition and processing after flow resumes varies with river morphology and the magnitude of the flow pulse[16]. However, except during extreme flow conditions, much of the mobilized litter will remain in the river channels and riparian areas, where it decomposes at rates similar to those in perennial rivers. As these rates are much faster than those in upland terrestrial sites[1,14], these findings suggest that to neglect IRES leads to a notable underestimation of the contribution of the world's river network to the total global CO_2 flux to the atmosphere. Our study suggests that, in addition to the globally relevant amounts of CO_2 released from IRES during both dry[26] (Supplementary Material 7b) and flowing phases, rewetting events act as control points[27]. This implies an upward revision of organic matter transformations and CO_2 emissions from river networks on the global scale. Indeed, based on the comparison of daily CO_2 emission rates with those reported from perennial rivers and streams, IRES could increase estimates of global CO_2 emissions from streams and rivers by 7–152%, the CO_2 released from LL during a single rewetting event alone contributing roughly from 3 to 10% of this increase (Supplementary Material 7a). Similarly, taking IRES into account would improve estimates of the consequences of global climate change on C cycling given that the spatial extent of IRES will increase, and periods of drying will become more prolonged in many regions[9,11,13].

The data and conceptual framework presented here provide the basis needed to develop models of litter decomposition and C cycling in fresh waters that include IRES. The next steps are to quantify CO_2 emissions upon flow resumption in situ[16] and collect data on LL quantity and decomposability for continental and other climates that are not well represented at present. CO_2 emissions from dry phases, suggested recently to be substantial[26], along with those from flowing phases[3] need to be integrated with those during wetting events, and temporal variability (including its dependency on other environmental conditions, such as temperature) must be studied for extended periods after flow resumes to build adequate quantitative models of global C cycling that consider

the spatiotemporal dynamics of IRES under the present and future climatic conditions.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at https://doi.org/10.1038/s41561-018-0134-4.

Received: 6 October 2017; Accepted: 17 April 2018;
Published online: 21 May 2018

References

1. Boyero, L. et al. A global experiment suggests climate warming will not accelerate litter decomposition in streams but might reduce carbon sequestration. *Ecol. Lett.* **14**, 289–294 (2011).
2. Beer, C. et al. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* **329**, 834–838 (2010).
3. Raymond, P. A. et al. Global carbon dioxide emissions from inland waters. *Nature* **503**, 355–359 (2013).
4. Hotchkiss, E. R. et al. Sources of and processes controlling CO_2 emissions change with the size of streams and rivers. *Nat. Geosci.* **8**, 696–699 (2015).
5. Gessner, M. O. et al. Diversity meets decomposition. *Trends Ecol. Evol.* **25**, 372–380 (2010).
6. Battin, T. J. et al. The boundless carbon cycle. *Nature* **2**, 598–600 (2009).
7. Butman, D. et al. Aquatic carbon cycling in the conterminous United States and implications for terrestrial carbon accounting. *Proc. Natl Acad. Sci. USA* **113**, 58–63 (2016).
8. Datry, T., Corti, R., Foulquier, A., von Schiller, D. & Tockner, T. One for all, all for one: a global river research network. *Eos* **97**, 13–15 (2016).
9. Larned, S. T., Datry, T., Arscott, D. B. & Tockner, K. Emerging concepts in temporary-river ecology. *Freshw. Biol.* **55**, 717–738 (2010).
10. Stanley, E. H., Fisher, S. G. & Grimm, N. B. Ecosystem expansion and contraction in streams. *BioScience* **47**, 427–435 (1997).
11. Datry, T., Larned, S. T. & Tockner, K. Intermittent rivers: a challenge for freshwater ecology. *BioScience* **64**, 229–235 (2014).
12. Acuña, V. et al. Why should we care about temporary waterways? *Science* **343**, 1080–1081 (2014).
13. Jaeger, K. L., Olden, J. D. & Pelland, N. A. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proc. Natl Acad. Sci. USA* **111**, 13894–13899 (2014).
14. Foulquier, A., Artigas, J., Pesce, S. & Datry, T. Drying responses of microbial litter decomposition and associated fungal and bacterial communities are not affected by emersion frequency. *Freshw. Sci.* **34**, 1233–1244 (2015).
15. Austin, A. T. & Vivanco, L. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* **442**, 555–558 (2006).
16. Corti, R. & Datry, T. Invertebrates and sestonic matter in an advancing wetted front travelling down a dry river bed (Albarine, France). *Freshw. Sci.* **31**, 1187–1201 (2012).
17. Rosado, J., Morais, M. & Tockner, K. Mass dispersal of terrestrial organisms during first flush events in a temporary stream. *River Res. Appl.* **31**, 912–917 (2015).
18. Michaletz, S. T., Cheng, D., Kerkhoff, A. J. & Enquist, B. J. Convergence of terrestrial plant production across global climate gradients. *Nature* **512**, 39–43 (2014).
19. Ehrman, T. P. & Lamberti, G. A. Hydraulic and particulate matter retention in a 3rd-order Indiana stream. *J. N. Am. Benthol. Soc.* **11**, 341–349 (1992).
20. Boyero, L. et al. Riparian plant litter quality increases with latitude. *Sci. Rep.* **7**, 10562 (2017).
21. Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. & Cushing, C. E. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**, 130–137 (1980).
22. Olson, J. S. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* **44**, 322–331 (1963).
23. Aerts, R. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* **79**, 439–449 (1997).
24. Cleveland, C. C., Neff, J. C., Townsend, A. R. & Hood, E. Composition, dynamics, and fate of leached dissolved organic matter in terrestrial ecosystems: results from a decomposition experiment. *Ecosystems* **7**, 175–285 (2004).
25. Hasler, C. T., Butman, D., Jeffrey, J. D. & Suski, C. D. Freshwater biota and rising pCO_2? *Ecol. Lett.* **19**, 98–108 (2016).
26. Gómez-Gener, L. et al. When water vanishes: magnitude and regulation of carbon dioxide emissions from dry temporary streams. *Ecosystems* **19**, 710–723 (2016).
27. Bernhardt, E. S. et al. Control points in ecosystems: moving beyond the hot spot hot moment concept. *Ecosystems* **20**, 665–682 (2017).
28. Benstead, J. P. & Leigh, D. S. An expanded role for river networks. *Nat. Geosci.* **5**, 678–679 (2012).
29. Leigh, C. et al. Ecological research and management of intermittent rivers: an historical review and future directions. *Freshw. Biol.* **61**, 1181–1199 (2016).
30. Stubbington, R., England, J., Wood, P. J. & Sefton, C. E. Temporary streams in temperate zones: recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. *WIRES Water* **4**, e1223 (2017).
31. Datry, T., Bonada, N. & Boulton, A. J. (eds) in *Intermittent Rivers and Ephemeral Streams: Ecology and Management* 1–20 (Academic, Oxford, 2017).
32. Snelder, T. H. et al. Regionalization of patterns of flow intermittence from gauging station records. *Hydrol. Earth Syst. Sci.* **17**, 2685–2699 (2013).
33. Tooth, S. Process, form and change in dryland rivers: a review of recent research. *Earth Sci. Rev.* **51**, 67–107 (2000).
34. Levick, L. R. et al. *The Ecological and Hydrological Significance of Ephemeral and Intermittent Streams in the Arid and Semi-arid American Southwest* (US Environmental Protection Agency, Washington DC, 2008).
35. Huston, M. A. & Wolverton, S. The global distribution of net primary production: resolving the paradox. *Ecol. Monogr.* **79**, 343–377 (2009).
36. Murphy, P. G. & Lugo, A. E. Ecology of tropical dry forest. *Ann. Rev. Ecol. Syst.* **17**, 67–88 (1986).
37. De Deyn, G. B., Cornelissen, J. H. C. & Bardgett, R. D. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol. Lett.* **11**, 516–531 (2008).

Acknowledgements

This study was made possible thanks to a large collective effort of a global research network entitled the "1000 Intermittent River Project" (1000IRP) that merges individual knowledge, forces and passion through simple, consistent and comparable joint field experiments worldwide.

Author contributions

T.D., A.F., R.C., D.vS. and K.T. assumed responsibility for the overall project planning and coordination. All authors collected plant litter in their countries and processed and analysed this material. The centralized lab analyses were conducted by T.D., A.F., R.C., C.M.-L. and J.C.C. The data compilation and database management was carried out by R.C. and C.M.-L. The data analyses were performed by T.D., A.F., R.C. and C.M.-L. T.D. led the writing of the manuscript with A.F. and notable contributions by M.O.G., B.G., M.Moleón and R.Stubbington. All the other authors commented on and contributed to revising draft versions.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41561-018-0134-4.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to T.D.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

[1]IRSTEA, UR RiverLy, Centre de Lyon-Villeurbanne, Villeurbanne, France. [2]UMR 'BOREA' CNRS 7208/IRD 207/MNHN/UPMC, DMPA, Museum National d'Histoire Naturelle, Paris, France. [3]Universite Grenoble Alpes, Laboratoire d'Écologie Alpine (LECA), UMR CNRS-UGA-USMB, Grenoble, France. [4]Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country (UPV/EHU), Bilbao, Spain. [5]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany. [6]Institute of Biology, Freie Universität Berlin, Berlin, Germany. [7]Université Savoie Mont Blanc, INRA, CARRTEL, Thonon-Les Bains, France. [8]Department of Ecology, Berlin Institute of Technology (TU Berlin), Berlin, Germany. [9]Department of Zoology, University of Granada, Granada, Spain. [10]School of Science and Technology, Nottingham Trent University, Nottingham, UK. [11]Department of Geosciences, Federal University of São João del-Rei, São João del-Rei, Brazil. [12]Laboratorio de Fotobiología, INIBIOMA (U.N.COMAHUE - CONICET), Bariloche, Argentina. [13]Department of Biology, University of Oklahoma, Norman, OK, USA. [14]Department of Evolutionary Biology and

Environmental Studies, University of Zurich, Zürich, Switzerland. [15]Zuckerberg Institute for Water Research, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer, Israel. [16]Université de Lorraine - UR AFPA, Vandoeuvre-Les-Nancy, France. [17]Faculty of Environmental Science, Center of Environmental Science EULA-Chile and CHRIAM Center, Universidad de Concepción, Concepción, Chile. [18]Department of Geography, University of California, Berkeley, CA, USA. [19]Edith Cowan University, School of Science, Mine Water and Environment Research Centre (MiWER), Joondalup, Victoria, Australia. [20]Group of Lotic Ecology (ELICE-RESTORES), Instituto de Biología, Universidad de Antioquia, Medellín, Colombia. [21]Department of Environment and Science, Queensland Government, Brisbane, Queensland, Australia. [22]Department of Geosciences, Federal University of São João del-Rei, São João del-Rei, Brazil. [23]Department of Biology, University of San Diego, San Diego, CA, USA. [24]School of Natural Resources and the Environment, University of Arizona, Tucson AZ, USA. [25]Grup de Recerca Freshwater Ecology and Management (FEM), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Spain. [26]Murray-Darling Freshwater Research Centre, La Trobe University, Wodonga, Australia, Victoria. [27]Faculty of Environmental Science, Center of Environmental Science EULA-Chile and CHRIAM Center, Universidad de Concepción, Concepción, Chile. [28]Institute of Earth Sciences, University of Applied Sciences and Arts of Southern Switzerland, Canobbio, Switzerland. [29]Australian Rivers Institute, Griffith University, Nathan, Queensland, Australia. [30]Department of Environmental Biology, University of Navarra, School of Sciences, Pamplona, Spain. [31]Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Coimbra, Portugal. [32]Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, USA. [33]LIEC, UMR CNRS 7360, Université de Lorraine, Metz, France. [34]Centro de Ciências Agrárias e Biológicas, Universidade Estadual Vale do Acaraú, Sobral, Brazil. [35]Water Research Institute - National Research Council, Bari, Italy. [36]Unidad de Limnología y Recursos Acuáticos (ULRA), Universidad Mayor de San Simón, Cochabamba, Bolivia. [37]Department of Ecology and Hydrology, Regional Campus of International Excellence 'Campus Mare Nostrum' - University of Murcia, Murcia, Spain. [38]Institute for Applied Ecology, University of Canberra, Bruce, Territory Australian Capital, Australia. [39]Centre International de Recherche en Agronomie pour le Développement, CIRAD, UPR HORTSYS, Montpellier, France. [40]School of Biological Sciences, University of Canterbury, Christchurch, New Zealand. [41]INRA, UAR 1275 DEPT EFPA, Centre de recherche de Nancy, Champenoux, France. [42]School of Marine Sciences, Ruppin Academic Center, Michmoret, Israel. [43]Department of Biosciences, Mangalore University, Mangalore, India. [44]Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden. [45]MARE – Marine and Environmental Sciences Centre, Department of Life Sciences, University of Coimbra, Coimbra, Portugal. [46]Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main, Germany. [47]School of Biological and Chemical Sciences, Queen Mary University of London, London, UK. [48]Ezemvelo KZN Wildlife, Pietermaritzburg, South Africa. [49]Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parma, Italy. [50]Department of Aquatic Ecology, Eawag the Swiss Federal Institute of Aquatic Science and Technology, Duebendorf, Switzerland. [51]Institute for Ecological Chemistry, Plant Analysis and Stored Product Protection, Julius-Kuehn-Institute, Berlin, Germany. [52]Department of LimnologyUniversity of Münster, Institute for Evolution and Biodiversity, Münster, Germany. [53]Department of Biology, Faculty of Science, University of Zagreb, Zagreb, Croatia. [54]Department of Freshwater Invertebrates, Albany Museum, Grahamstown, South Africa. [55]Department of Biology, Universidade de Evora, Evora, Portugal. [56]Universidad Mayor, Real y Pontificia de San Francisco Xavier de Chuquisaca, Sucre, Bolivia. [57]Missouri University of Science and Technology, Rolla, MO, USA. [58]Terra Cypria - The Cyprus Conservation Foundation, Limassol, Cyprus. [59]Departamento de Ecología y Biología Animal, Universidad de Vigo, Vigo, Spain. [60]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic. [61]Department of Biology, University of Montenegro, Podgorica, Montenegro. [62]Department of Biology and Ecology, Faculty of Sciences and Mathematics, University of Niš, Nis, Serbia. [63]National Institute of Water and Atmospheric Research, Hamilton, New Zealand. [64]Laboratoire d'Écologie et Gestion des Ecosystèmes Naturels (LECGEN), University of Tlemcen, Tlemcen, Algeria. [65]Israel Nature & Parks Authority, Jerusalem, Israel. [66]Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA. [67]Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER) Freshwater Ecology Research Group College of Science and Engineering, James Cook University, Townsville, Queensland, Australia. [68]Center for Applied Geosciences, Eberhard Karls Universität Tübingen, Tübingen, Germany. [69]Department of Bioscience, Aarhus University, Silkeborg, Denmark. *e-mail: Thibault.datry@irstea.fr

Methods

Sampling design. TPL deposited on dry riverbeds was collected by the participants of an international consortium (http://1000_intermittent_rivers_project.irstea.fr) following a standardized protocol. In total, 212 near-natural river reaches were studied in 22 countries that spanned 13 Köppen–Geiger climate classes (Supplementary Material 2). Briefly, the sampled river reaches were ten times the average active channel widths to cover a representative area of each river channel and to ensure a consistent sampling effort across reaches[38]. The active channel was defined as the area of frequently inundated and exposed riverbed sediments between established edges of perennial terrestrial vegetation and/or abrupt changes in the slope[39]. TPL was collected by hand from 1 m^2 quadrats placed randomly within each reach during a dry phase. The quadrats covered ~5% of the reach surface area (for example, five quadrats in a 100 m^2 reach). Different types of TPL (that is, leaves, wood, fruits, catkins and herbs) were stored in separate airtight plastic bags.

Environmental variables. A set of 22 environmental variables that reflect reach characteristics at different spatial scales was estimated or calculated for each site (Supplementary Material 8). Of these, 17 variables were determined locally. The mean annual temperature and precipitation were extracted from the WorldClim database (www.worldclim.org), which gives 1 km spatial resolution climate surfaces for global land areas over the period 1970–2000. The mean annual PET and mean annual aridity were determined using the Global Aridity and PET database published by the Consortium for Spatial Information (www.cgiar-csi.org) using the WorldClim.org database. PET is a measure of the ability of the atmosphere to remove water through evapotranspiration and was calculated as a function of annual mean temperature, daily temperature range and extraterrestrial radiation between 1950 and 2000. The mean annual aridity was assessed using an aridity index[40] and expressed as 1,000 × precipitation/PET between 1950 and 2000. Aridity index values were high in humid and low in arid conditions. Climate zones in the Köppen–Geiger system were determined from the global climate map derived from long-term monthly precipitation and temperature time series in a grid of weather stations and interpolated among stations using a two-dimensional (latitude and longitude) thin-plate spline with tension onto a 0.1° × 0.1° grid for each continent[41]. Last, we estimated the time since leaf abscission as the time between the estimated onset of leaf senescence and the sampling date. Although leaf fall is more continuous in tropical areas than in other climate zones, to facilitate the comparison among sites the onset of leaf senescence was set to 1 September and 15 February in the northern and southern hemispheres, respectively[42].

Litter drying, weighing and grinding. TPL was transported to local laboratories within 8 h of collection when possible and oven dried at 60 °C for ≥12 h (<24 h for leaves). Fresh material, such as fruits or wood, was dried at room temperature for 1 week before oven drying. The dried material was weighed to the nearest gram. Although wood can account for considerable volumes of TPL deposited in riverbeds, it is far more recalcitrant than LL. Therefore, we focused on LL in our assessment of TPL decomposability during short-term rewetting events. LL was thoroughly mixed before taking a 60 g subsample that was first shredded by hand and passed through a 0.5 cm mesh screen and then shipped to the IRSTEA (Institut national de recherche en sciences et technologies pour l'environnement et l'agriculture) laboratory for further processing.

Decomposability of LL. Laboratory measurements can provide a useful means to address global-scale environmental research questions[43] and overcome the current data shortage on IRES. In particular, they facilitate tests of between-reach variability in O_2 consumption rates in a standardized way and the identification of the primary drivers responsible for the observed variability. Although we did not quantify decomposition rates directly, we assessed two proxies of LL decomposability, the C:N mass ratio and oxygen (O_2) consumption rate after rewetting.

Three 10 mg LL subsamples were taken from each sample, ground to 5 µm with a ball mill (MM301 (Retsch GmbH) and the C:N ratio determined with an elemental analyser (FlashEA 1112 (Fisher Scientific). O_2 consumption was determined in respiration flasks placed in a climatic room at 20 °C. LL subsamples were processed in 10 successive batches of 25–50 subsamples. Each batch was incubated in three 200 l polyethylene containers filled with tap water at room temperature to prevent O_2 exchange with the atmosphere. For each subsample, two analytical replicates were processed by placing 0.1 g of LL into 250 ml glass respiration flasks filled with Volvic mineral water, and then sealed airtight using a 3.2 mm thick silicon–polytetrafluoroethylene septum and a cut-out open-top cap. Care was taken to ensure that air bubbles were excluded. O_2 concentrations were measured with a needle-based micro-optode (Oxygen Microsensor PM-PSt7 (PreSens)) using a stand-alone, portable, fibreoptic O_2 meter (Microx 4 trace (PreSens)). Incubations were run for approximately 24 h (range of incubation times from 23.4 to 25.8 h, mean ± s.d. = 24.3 ± 2.0 h) to simulate short-term rewetting events. We used LL communities as a source of microbes because dry LL hosts dormant communities that can quickly resume activity after litter rewetting[44]. We also ran tests to ensure our oxygen consumption rates were realistic. This was achieved by using LL and different sources of water with and without a standard inoculum from local streams (see below).

O_2 concentrations were measured twice, 2 h and 24 h after the respiration flasks were filled with water. We waited for 2 h before taking the first measurement to allow gas release from air-saturated pores within the LL[45]. Although the respiration flasks were carefully filled without bubbling the water, we left them open for 2 h while the LL released gas, to ensure that the O_2 concentration was saturated, but not supersaturated, to avoid a notable underestimation of respiration rates over 24 h. Flasks were gently agitated every 6 h during the incubation period and before each measurement to ensure homogeneous O_2 concentrations in the water. For each batch, O_2 concentrations were also measured in three control respiration flasks filled with Volvic mineral water only. Microbial respiration associated with LL (R (mg O_2 g^{-1} LL dry mass h^{-1})) was calculated as:

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

where O_2 is the dissolved O_2 concentration (mg l^{-1}), the subscripts sample and control refer to each analytical replicate and the mean O_2 of the three control respiration flasks and the superscripts 2h and 24h correspond to the O_2 concentrations measured 2 h and 24 h after the flask was filled, respectively. R was then standardized to 20 °C to correct for small (that is, ±1.1 °C) temperature variations during the measurements, assuming that the O_2 consumption rates double with a temperature increase of 10 °C (ref. [46]). The mean of the two analytical replicates was used as a measure of microbial respiration associated with LL rewetting for each sample. For ten samples, we did not have sufficient litter material to conduct the respiration measures, and for another six the material was not adequately processed by the collectors and was thus excluded from the analysis. Hence, the total number of samples analysed for O_2 consumption rates was 196 (Supplementary Material 9).

The total potential CO_2 released per m^2 of riverbed over 24 h after rewetting was estimated by multiplying, for each sampling site, the amount of accumulated LL (g m^{-2}) by the rate of O_2 consumption (mg O_2 g^{-1} LL dry mass h^{-1}) over 24 h (Supplementary Material 9). The obtained estimates of O_2 consumption (mg O_2 m^{-2} day^{-1}) were then converted into CO_2 production (mg CO_2 m^{-2} day^{-1}) by assuming a respiratory quotient of 1 (ref. [47]).

Sensitivity of O_2 consumption measurements. To explore the sensitivity of our laboratory protocol to assess LL respiration in the initial stage of rewetting, we compared O_2 consumption rates with and without a microbial inoculum added (Supplementary Material 10). The inoculum was prepared from sediments collected with a shovel from a flowing reach of the Albarine River close to Lyon[14]. We added 250 ml of Volvic water to 250 ml of sediment and placed it twice in an ultrasonic bath (Branson 5510E (Emerson)) for 30 s. The suspension of water and sediment was gently shaken after ultrasonication. We then added 2.5 ml of the inoculum suspension to each respiration flask before filling them with Volvic water. Before adding the inoculum, the suspension was gently shaken again to ensure a uniform inoculum distribution within the flask. In addition, we compared oxygen consumption rates without inoculum by using stream water from three LL collection sites (Albarine, Audeux and Calavon) instead of Volvic mineral water (Supplementary Material 10). We did not use an inoculum in our final experiments because: (1) it is conceptually problematic to use an inoculum from one system to quantify the decomposability of material from other areas and the large variability induced by doing so could mask large-scale patterns of oxygen-consumption rates upon rewetting; (2) it was impractical to ask international participants to send 2–3 l of river water to IRSTEA, especially when the rivers were dry; (4) it is virtually impossible to keep an inoculum constant among runs in laboratory microcosms. By not adding an inoculum, our O_2 consumption rates were probably underestimated (that is, conservative) relative to the in situ rates of O_2 consumption (Supplementary Material 10).

Data analysis. We used RF models to explore the relationships between environmental variables and TPL quantity, LL decomposability and CO_2 release upon rewetting events. RF models are highly flexible regression techniques suitable for modelling response variables (for example, the quantity and decomposability of TPL) that show complex relationships with environmental variables (for example, climate, riparian zone, flow regime and channel topography). RF models are invariant to monotonic transformations of environmental variables, perform better than other regression techniques when facing multicollinearity, are relatively robust to overfitting, automatically fit non-linear relationships and high-order interactions, and provide an overall goodness-of-fit measure (R^2) and a measure of the importance of each variable in a model[48–50].

The role of the environmental variables in RF models can be examined using importance measures and partial dependence plots. Importance measures provide the contribution of variables to model the accuracy and are obtained from the degradation in model performance when a predictor is randomly permutated[48,50]. Partial dependence plots show the marginal contribution of a variable to the response (that is, the response as a function of the variable when the other variables are held at their mean value[48–50]) and were used to interpret the relationships between predictors and dependent variables (responses),

which were $\log_{10}(x + 1)$ transformed prior to analyses. Sets of global RF models were run for the main dependent variables (quantities of TPL and LL; LL C:N, respiration rate and CO_2 production) and then these RF sets were run for each of three climate zones using the Köppen–Geiger classification of sampling sites: arid (merging Köppen–Geiger BSh, BSk, BWh and BWk; $n = 31$), temperate (merging Cfa, Cfb, Csa, Csb and Cwa; $n = 150$) and tropical (merging As and Aw; $n = 19$). No RF models were run for alpine and continental climates due to the low number (≤ 10) of sampling sites.

We ran all the global and climate-specific models with and without time since senescence as a predictor to assess the potential of this variable to improve predictive power despite the large uncertainty of this variable in some climate zones, particularly in the tropics. Removing the variable from the models did not improve or diminish the predictive power, including that for IRES in the tropics, but as the RF models selected it as a strong predictor for most response variables, we decided to include it in the analyses. The threshold to assess statistical significance was 0.05 for all the analyses, which were conducted in R 3.3.3 (ref. [51]) using the 'RandomForest' package[52].

Data availability. The presented data are available on the figshare repository under the https://doi.org/10.6084/m9.figshare.6078734.

References

38. Leopold, L. B. *Channel and Hillslope Processes in a Semiarid Area, New Mexico* (Department of the Interior, Washington DC, 1966).
39. Gordon, N. D, McMahon, T. A., Finlayson, B. L., Gippel, C. J. & Nathan, R. J. *Stream Hydrology. An Introduction for Ecologists* 2nd edn (John Wiley & Sons, Hoboken, 2004).
40. *World Atlas of Desertification* 2nd edn (UNEP, 1997).
41. Peel, M. C., Finlayson, B. L. & McMahon, T. A. Updated world map of the Köppen–Geiger climate classification. *Hydrol. Earth Syst. Sci.* **11**, 1633–1644 (2007).
42. Estiarte, M. & Peñuelas, J. Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency. *Glob. Change Biol.* **21**, 1005–1017 (2015).
43. Benton, T. G., Solan, M., Travis, J. M. & Sait, S. M. Microcosm experiments can inform global ecological problems. *Trends Ecol. Evol.* **22**, 516–521 (2007).
44. Mora-Gómez, J. et al. Microbial decomposition is highly sensitive to leaf litter emersion in a permanent temperate stream. *Sci. Total Environ.* **621**, 486–496 (2018).
45. Dorca-Fornell, C. et al. Increased leaf mesophyll porosity following transient retinoblastoma-related protein silencing is revealed by microcomputed tomography imaging and leads to a system-level physiological response to the altered cell division pattern. *Plant J.* **76**, 914–929 (2013).
46. Davidson, E. A. & Janssens, I. A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165–173 (2006).
47. Dilly, O. Microbial respiratory quotient during basal metabolism and after glucose amendment in soils and litter. *Soil Biol. Biochem.* **33**, 117–127 (2001).
48. Pitcher, R. C. et al. Exploring the role of environmental variables in shaping patterns of seabed biodiversity composition in regional-scale ecosystems. *J. Appl. Ecol.* **49**, 670–679 (2012).
49. Breiman, L. Random forests. *Mach. Learn.* **45**, 5–32 (2001).
50. Leigh, C. & Datry, T. Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis. *Ecography* **40**, 487–499 (2017).
51. R. Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2017).
52. Liaw, A. & Wiener, M. Classification and regression by Random Forest. *R News* **2**, 18–22 (2002).