View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by Nottingham Trent Institutional Repository (IRep)

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

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

[1]UR RiverLy, centre de Lyon-Villeurbanne, 5 rue de la Doua CS 20244, 69625 Villeurbanne, France [2] UMR "BOREA" CNRS 7208/IRD 207/MNHN/UPMC, DMPA, Museum National d'Histoire Naturelle, Paris Cedex, France. [3]Université Grenoble Alpes, Laboratoire d'Écologie Alpine (LECA), UMR CNRS-UGA-USMB 5553, Grenoble, France. [4]Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country (UPV/EHU), P.O. Box 644, 48080-Bilbao, Spain. [5]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany. [6]Institute of Biology, Freie Universität Berlin, Germany. [7]Université Savoie Mont Blanc, INRA, CARRTEL, 74200, Thonon-Les Bains, France. [8]Department of Ecology, Berlin Institute of Technology (TU Berlin), Ernst-Reuter-Platz 1, 10587 Berlin, Germany. [9]Department of Zoology, University of Granada, Avda. de Fuente Nueva, s/n, 18071-Granada, Spain. [10]School of Science and Technology, Nottingham Trent University, UK. [11]Department of Geosciences, Federal University of São João del-Rei, Campus Tancredo Neves, 36301-360 São João del-Rei, MG, Brazil. [12]Laboratorio de Fotobiología, INIBIOMA (U.N.COMAHUE - CONICET), Bariloche, Argentina. [13]University of Oklahoma, Department of Biology, Norman, OK, 73019 USA. [14]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstr. 190, CH-8057 Zürich, Switzerland. [15]Zuckerberg Institute for Water Research, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer, 84990, Israel. [16]Université de Lorraine - UR AFPA, 54505 Vandoeuvre-Les-Nancy, France. [17]Department of Aquatic Systems, Faculty of Environmental Science and EULA Chile Centre, Universidad de Concepción, Casilla 160-C, Concepción, Chile. [18]Department of Geography, University of California, Berkeley, CA 94720, USA. [19]Edith Cowan University, School of Science, Mine Water and Environment Research Centre (MiWER), Australia. [20]Instituto de Biología, Universidad de Antioquia, Medellín, Colombia. [21]Department of Science, Information Technology and Innovation, Queensland Government, Australia. [22]Department of Geosciences, Federal University of São João del-Rei, Campus Tancredo Neves, 36301-360 São João del-Rei, MG, Brazil. [23]University of San Diego, Department of Biology, San Diego, CA 92110, USA. [24]School of Natural Resources and the Environment, University of Arizona, 1064 E lowelll street room N326 Tucson, AZ 85721, 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 (UB), Diagonal 643, 08028-Barcelona, Catalonia, Spain. [26]Murray-Darling Freshwater Research Centre, La Trobe University, Wodonga, Victoria, 3689, Australia. [27]Faculty of Environmental Science and EULA Chile Centre, Universidad de Concepción, Casilla 160-C, Concepción, Chile. [28]Institute of Earth Sciences, University of Applied Sciences and Arts of Southern Switzerland, Campus Trevano, 6952 Canobbio, Switzerland. [29]Australian Rivers Institute, Griffith University, Nathan, Queensland, Australia. [30]University of Navarra, School of Sciences, Department of Environmental Biology, Irunlarrea 1, 31080-Pamplona, Spain. [31]Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal. [32]Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, USA. [33]LIEC, UMR CNRS 7360, Université de Lorraine, Metz, France. [34]Centro de Ciências Agrárias e Biológicas, Universidade Estadual Vale do Acaraú, Sobral, CE, Brazil. [35]Water Research Institute - National Research Council, Italy. [36]Unidad de Limnología y Recursos Acuáticos (ULRA), Universidad Mayor de San Simón,

Casilla de Correos 992, Cochabamba, Bolivia. [37]Department of Ecology and Hydrology, Regional Campus of International Excellence "Campus Mare Nostrum" - University of Murcia, Campus de Espinardo, 30100-Murcia, Spain. [38]Institute for Applied Ecology, University of Canberra, Bruce, ACT 2601, Australia. [39]Centre International de Recherche en Agronomie pour le Développement, CIRAD, UPR HORTSYS, F-34398 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, 40297 Michmoret, Israel. [43]Department of Biosciences, Bangalore University, Mangalore 574 199, Karnataka, 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, 3004-517 Coimbra, Portugal. [46]Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany. [47]School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK. [48]Ezemvelo KZN Wildlife, 1 Peter Brown drive, Pietermaritzburg, KwaZulu-Natal, South Africa. [49]Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parco Area delle Scienze 11/A – 43124 Parma, Italy.[50]Department of Aquatic Ecology, Eawag the Swiss Federal Institute of Aquatic Science and Technology, Ueberlandstrasse 133, 8600 Duebendorf, Switzerland.[51]Institute for Ecological Chemistry, Plant Analysis and Stored Product Protection, Julius-Kuehn-Institute, Koenigin-Luise-Str. 19, 14195 Berlin, Germany. [52]University of Münster, Institute for Evolution and Biodiversity, Department of Limnology, Hüfferstr. 1, 48149 Münster, Germany. [53]Department of Biology, Faculty of Science, University of Zagreb, Croatia. [54]Albany Museum, Department of Freshwater Invertebrates, Somerset Street, Grahamstown, 6140, South Africa. [55]Department of Biology, Universidade de Evora, Evora, Portugal. [56]Universidad Mayor, Real y Pontificia de San Francisco Xavier de Chuquisaca, Bolivia. [57]Missouri University of Science and Technology, USA. [58]Terra Cypria - The Cyprus Conservation Foundation, Cyprus. [59]Departamento de Ecología y Biología Animal, Universidad de Vigo, 36310-Vigo, Spain. [60]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic. [61]Department of Biology, University of Montenegro, Cetinjski put b.b., 81000 Podgorica, Montenegro. [62]Department of Biology and Ecology, Faculty of Sciences and Mathematics, University of Niš, Višegradska 33, 18000 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, 13000 Tlemcen, Algeria. [65]Israel Nature & Parks Authority, Israel. [66]Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA. [67]Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER) Freshwater Ecology Research Group College of Science and Engineering, James Cook University, Townsville, 4811, Australia. [68]Department of Bioscience, Aarhus University, Vejlsøvej, 8600 Silkeborg, Denmark. [69]Center for Applied Geosciences, Eberhard Karls Universität Tübingen, Tübingen, Germany. *e-mail: Thibault.datry@irstea.fr

Statistics

Main text: 3000 words

Reference: 37 (and 19 in methods)

2 tables and 3 figures, 10 Supplementary Materials

Keywords: global change, river ecosystem functioning, CO_2 emissions, temporary rivers, riparian vegetation, C cycle

Perennial rivers and streams make a disproportionate contribution to global carbon (C) cycling. However, the contribution of intermittent rivers and ephemeral streams, 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 accumulate in dry riverbeds and, upon rewetting, this material can undergo rapid microbial processing. We present the results of a global research collaboration which collected and analysed terrestrial plant litter from 212 dry riverbeds spanning major environmental gradients and climate zones. We assessed litter decomposability by quantifying the litter C-to-nitrogen ratio (C:N) and oxygen (O_2) consumption in standardised assays and estimated 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 intermittent rivers and ephemeral streams. Our estimates indicate that a single pulse of CO_2 emission upon litter rewetting contribute up to 10% of daily CO_2 emission from perennial rivers and stream, particularly from temperate climates. This implies that the contributions of intermittent rivers and ephemeral streams should be included in global C cycling assessments.

Decomposition of terrestrial plant litter is an essential, biosphere-scale ecosystem process[1]. Of 120 Pg of organic 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 terrestrial plant litter (TPL) decomposition and atmospheric CO_2 emissions[3,4]. This contribution is particularly apparent in perennial rivers and streams, where water and nutrient availability stimulate 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, including 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[8,9,10]. IRES are widespread ecosystems draining a large proportion of terrestrial biomes across all continents and climate types[9,12]. 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 mobilised and transported downstream[16,17] (**Supplementary Material 1**). Concentrations of particulate and dissolved organic matter in advancing wetted fronts exceed baseflow concentrations by several orders of magnitude[16]. IRES have therefore been conceptualised as punctuated biogeochemical reactors[9].

To understand the role of IRES in global C cycling, global-scale data are needed to characterise the variables controlling TPL 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, including the timing and duration of dry periods[14], control TPL deposition and retention, with wide channels receiving proportionally less riparian material than narrow ones[19]. TPL decomposability is typically altered during dry phases, due to 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 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 zones[8] (**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 $\pm$ S.D. = 277 $\pm$
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 $\pm$ S.D.
166 = 88 $\pm$ 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

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 dry period duration increased to 200 d, and then dropped sharply (**Fig. 2**). The quantity of LL fell for 320 days after 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, suggesting 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 regarding the fate of TPL entering river channels. According to the RCC, a large portion of TPL entering forested headwaters is immediately processed by heterotrophic microbes and invertebrate shredders, generating 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 perennial rivers[8,14], because the absence of flowing water limits biological activity and physical abrasion. During the initial phases when flow resumes, much of this material can then be transported and further processed downstream[9,10,16].

Overall, LL accumulation in IRES matches global patterns in terrestrial inputs[1,20], revealing 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], while the saturating relationship observed above an index value of 700 suggest 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. Downstream effects of LL transport and processing

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

Decomposability of accumulated leaf litter

The mass C:N ratio of LL, as a first proxy of decomposability, ranged from 17 to 154 (mean ± S.D. = 46 ± 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 $year^{-1}$ and then gradually decreased (**Supplementary Material 3**). The C:N ratio decreased with riparian cover and the aridity index, the latter relationship resembling 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, including tropical conditions, compared to other climate types[20,23]. More research is needed to determine how plant species richness, vegetation structure and functional diversity in riparian zones affect the C:N and decomposability of LL in dry riverbeds.

Decomposability was also related to 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 after ~100 days before C:N declined again, levelling 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, resulting in litter composed mostly of nutrient-poor structural compounds such as cellulose and lignin[24]. The initial decomposability of LL falling

onto dry riverbeds and subsequent quality changes affect decomposition in both the receiving and downstream reaches[16]. Thus, climate change-related extensions of dry periods[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 leaf litter 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 $\pm$ S.D. = 0.36 $\pm$ 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 metabolised 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, 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 $\pm$ S.D. = 0.88 $\pm$ 1.51, 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 10-fold 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 (min = 0%, mean = 3-10%, max = 47-152%; **Supplementary Material 7a**). This is remarkable, especially since 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 characterised neither by the highest O_2 consumption rates nor by the highest quantities of accumulated LL, indicating 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 (**Table 2, Fig. 3a**). Relationships were typically non-monotonic. The CO_2 released decreased sharply until 85 days after estimated senescence, before remaining relatively low and stable (**Fig. 3a**). CO_2 release decreased till an aridity index value of 230, then increased sharply till 700 to decrease again and stabilise at values above 800 (**Fig. 3a**). Last, rates of CO_2 release remained stable for 200 d of dry riverbeds, but sharply decreased thereafter (**Fig. 3a**). Although IRES release CO_2 during both flowing[3,25] and dry[26] phases, our study suggests that early stages of rewetting can be considered hot moments[9,11] or control points[27] of CO_2 release.

278 This finding is important because global estimates of CO_2 release focusing on perennial
279 rivers[3,4,7,25] have missed emissions from at least 84,000 km^2 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 $\pm$ 152, median = 41 g dry mass m^{-2}) than those in the tropics
286 (mean $\pm$ S.D. = 32 $\pm$ 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 research[29] 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 France[32] and up to 96% in the arid south-western USA[33, 34]. Tropical IRES often have higher
298 annual LL inputs than temperate forests[35], but our ability to predict their LL accumulation in
299 these riverbeds was reduced, probably because of often continuous leaf fall[36]. 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.

Our findings on LL accumulation were paralleled 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, 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 spanning 212 reaches on all continents (i) enabled us to document the extent of global variation in TPL and LL quantity and quality across dry riverbeds, and (ii) revealed 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], characterised by distinct phases of C accumulation and processing with much higher temporal variability in process rates than in perennial river ecosystems. Transport distance and site of litter deposition and processing after flow resumes will vary with river morphology and the magnitude of the flow pulse[16]. However, except during extreme flow conditions, much of the mobilised litter will remain in river channels and riparian areas, where it decomposes at rates similar to those in perennial rivers. Since these rates are much faster than in upland terrestrial sites[1,14], these findings suggest that neglecting 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 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 would imply 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**). Likewise, 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 period 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 would be 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) be studied for extended periods after flow resumes to build adequate quantitative models of global C cycling that consider the spatio-temporal dynamics of IRES under present and future climatic conditions.

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. *Freshwater 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. *Freshwater 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. Introduction. In *Intermittent Rivers and Ephemeral Streams: Ecology and Management* (eds. Datry, T., Bonada, N. & Boulton, A. J.) 1-20 (Academic Press, 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* (U.S. Environmental Protection Agency, 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) merging individual knowledge, forces and passion through simple, consistent and comparable joint field experiments worldwide.

Author contributions

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

Corresponding author: Correspondence and request for material should be addressed to Dr. Thibault Datry, IRSTEA Lyon, France. thibault.datry@irstea.fr

Competing interests

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

Table and Figure captions

Table 1: Quantity (g dry mass.m^{-2}) of terrestrial plant litter collected in dry riverbeds (Min: minimum, Max: maximum, Mean, S.D.: standard deviation, Fraction: % of the total quantity.

Table 2. Detailed results of global Random Forest (RF) models on five response variables. 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 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.

Figure 1. Main variables predicted to control plant litter accumulation and decomposability in intermittent rivers and ephemeral streams. The accumulation of terrestrial plant material is a function of the input of litter from riparian vegetation mediated by its retention that 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. Moléon (right panel).

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

Figure 3. a. Partial dependence of the probability of the CO_2 released by rewetted leaf litter (LL) over 24 h. Variables are shown from left to right in order of decreasing importance. The plots show the marginal contribution to probability of the CO_2 released by rewetted LL over 24 h (marginal response, y-axis) as a function of the predictors (i.e. 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.**

Methods

Sampling design. Terrestrial plant litter (TPL) deposited on dry riverbeds was collected by participants of an international consortium (http://1000_intermittent_rivers_project.irstea.fr[8]) following a standardised protocol. In total, 212 near-natural river reaches were studied in 22 countries spanning 13 Köppen-Geiger climate classes (**Supplementary Material 2**). Briefly, the sampled river reaches were 10 × the average active channel widths to cover a representative area of each river channel and to ensure 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 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 (e.g. five quadrats in a 100 m^2 reach). Different types of TPL (i.e. leaves, wood, fruits, catkins, herbs) were stored in separate airtight plastic bags.

Environmental variables. A set of 22 environmental variables reflecting reach characteristics at different spatial scales was estimated or calculated for each site (**Supplementary Material 8**). Seventeen variables were determined locally. Mean annual temperature and precipitation were extracted from the WorldClim.org database, which gives 1-km spatial resolution climate surfaces for global land areas over the period 1970-2000. Mean annual potential evapotranspiration (PET) and mean annual aridity were determined using the Global Aridity and PET database published by the Consortium for Spatial Information (CGIARCSI, http://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 extra-terrestrial radiation between 1950 and 2000. 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 following 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° by 0.1° grid for each continent[41]. Last, we estimated 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

comparison among sites, onset of leaf senescence was set to the 1st of September and the 15th of 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 leaf litter (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, then shipped to the IRSTEA laboratory (Lyon, France) for further processing.

Decomposability of leaf litter. Laboratory measurements can provide a useful means to address global-scale environmental research questions[43] and overcome the current data shortage on intermittent rivers and ephemeral streams. In particular, they facilitate tests of between-reach variability in O_2 consumption rates in a standardised way and 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, Haan, Germany) and the C:N ratio determined with an elemental analyzer (FlashEA 1112, Fisher Scientific, Waltham, Massachusetts, USA). 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 LL into 250-mL glass respiration flasks filled with Volvic® mineral water, then sealed airtight using a 3.2-mm-thick silicon-PTFE septum and a cut-out open-top cap. Care was taken to ensure air bubbles were excluded. O_2 concentrations were measured with a needle-based micro-optode (Oxygen Microsensor PM-PSt7; PreSens, Regensburg, Germany) using a stand-alone, portable, fiber-optic O_2 meter (Microx 4 trace; PreSens, Regensburg, Germany). Incubations were run for approximately 24 h (range of incubation times: 23.4-25.8 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, 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 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 homogenous 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:

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

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 2 h and 24 h correspond to the O_2 concentrations measured 2 h and 24 h after the flask was filled, respectively. *R* was then standardised to 20 °C to correct for small (i.e., ± 1.1°C) temperature variations during the measurements, assuming that O_2 consumption rates double with a temperature increase of 10 °C[46]. The mean of the two analytical replicates was used as a measure of microbial respiration associated with LL rewetting for each sample. For 10 samples, we had not sufficient litter material to conduct the respiration measures and for another 6, 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 (in g per m^2) by the rate of O_2 consumption (mg O_2 g^{-1} LL dry mass h^{-1}) over 24h (**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[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, France[14]. 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 O_2 consumption rates
604 were likely underestimated (i.e. conservative) relative to in-situ rates of O_2 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 CO_2 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 model[48-50].
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 value[48-50]) 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 CO_2 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 3.3.3[51] using the "RandomForest" package[52].

Data availability: The presented data are available on the FIGSHARE repository under the DOI: 10.6084/m9.figshare.6078734

Code availability: Not applicable.

References

38. Leopold, L. B. *Channel and Hillslope Processes in a Semiarid Area, New Mexico*. (Department of the Interior, U.S.A., 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, 2004).
40. UNEP (United Nations Environment Programme). *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). Available at: http://www.R-project.org (last accessed: July 1 2017).

52. Liaw, A. & Wiener, M. Classification and Regression by Random Forest. *R News* **2**, 18-22 (2002).