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# 1 **Does flood rhythm drive ecosystem responses in tropical riverscapes?**

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23

24 **Abstract**

25 Biotic communities are shaped by adaptations from generations of exposure to selective  
26 pressures by recurrent and often infrequent events. In large rivers, floods can act as significant  
27 agents of change, causing considerable physical and biotic disturbance while often enhancing  
28 productivity and diversity. We show that the relative balance between these seemingly divergent  
29 outcomes can be explained by the ‘rhythmicity’, or predictability of the timing and magnitude, of  
30 flood events. By analyzing biological data for large rivers that span a gradient of rhythmicity in  
31 the Neotropics and tropical Australia, we find that systems with rhythmic annual floods have  
32 higher fish species richness, more stable avian populations and elevated rates of riparian forest  
33 production compared with those with arrhythmic flood pulses. Intensification of the hydrological  
34 cycle driven by climate change, coupled with reductions in runoff due to water extractions for  
35 human use and altered discharge from impoundments, is expected to alter the hydrologic  
36 rhythmicity of floodplain rivers with significant consequences for both biodiversity and  
37 productivity.

38

39 **Key words:** rivers, biodiversity, productivity, stochasticity, determinism

40

41 **Introduction**

42 Many plant and animal phenologies and community-scale processes are aligned with  
43 annual cycles in abiotic factors such as temperature and day length (Foster and Kreitzman 2009,  
44 Helm et al. 2013). The predictable recurrence of annual events exerts strong selective pressures  
45 on individual species, resulting in adaptations to maximize fitness. Such systems may be  
46 described by deterministic models that consider how certain traits of a particular species allow it

47 to thrive under the existing set of environmental conditions, *i.e.* the niche (Clark 2008). If events  
48 are instead stochastic or unpredictable, selection will favor a different set of behavioral, life-  
49 history and morphological adaptations and species assemblages that may be better described by  
50 neutral models (Rosindell et al. 2012). Understanding the relative influence of deterministic and  
51 stochastic forces in shaping biological communities has long challenged ecologists (Gravel et al.  
52 2011).

53 River biotas are strongly influenced by flow regimes (Lytle and Poff 2004), which show  
54 considerable variation in predictability among rivers worldwide (Puckridge et al. 1998).  
55 Discharge patterns, including flood events, have often been severely modified by dams and  
56 diversions (Poff et al. 2007), and additional changes are predicted under climate change  
57 scenarios (Döll and Zhang 2010). Because the collective adaptations of species assemblages  
58 interact with environmental conditions to determine ecosystem structure and function (Lewis et  
59 al. 2000), other features of fluvial ecosystems will be influenced by changes in the predictability  
60 of flows (Sabo et al. 2010). Synthetic comparative efforts are needed to link the hydrologic  
61 properties of large floodplain rivers with biotic assemblages and their functions, including the  
62 provision of food and fiber for human societies (Tockner and Stanford 2002).

63 Ecosystem services derived from floodplains arise from the ‘flood-pulse advantage’, an  
64 enhancement of biological production in response to flooding (Junk et al. 1989). However, there  
65 is growing recognition that not all floods are ‘equal’ and differences in the magnitude and  
66 predictability of floods shape biological responses (Lytle and Poff 2004). Whilst seasonally  
67 predictable floods are important drivers of floodplain productivity in many systems (Winemiller  
68 2004), elsewhere, large, infrequent and unpredictable floods act as a major form of disturbance,  
69 capable of substantially moderating basin-scale productivity (Parsons et al. 2005). Thus, there is

70 a tension between the replenishing and damaging forces that arises from floods of differing  
71 magnitude and predictability (Lake et al. 2006). Despite recognition of this variability, there is  
72 no framework to evaluate patterns in productivity and biodiversity and how rivers and their  
73 floodplains may respond to human-induced alterations to flow, particularly at the basin scale  
74 (Palmer et al. 2008).

75 Here we quantify effects of flood regimes across structural/functional and  
76 aquatic/terrestrial dimensions to elucidate how hydrology controls the ecology of floods in large  
77 tropical rivers. We first evaluate the range of variation in river-floodplain rhythmicity across a  
78 gradient of large river basins from tropical latitudes, and then examine a set of ecological and  
79 biogeochemical properties associated with those rivers. Earlier approaches to conceptualize river  
80 ecosystems have been hampered by the lens through which biological features are viewed. As  
81 noted previously (Marcarelli et al. 2011), most studies have related abiotic drivers to either  
82 structural (e.g., patterns such as species diversity and food web linkages) or functional  
83 characteristics (e.g., processes such as biomass production and gas exchanges) separately rather  
84 than simultaneously relating abiotic drivers to multiple biotic properties. Further, the spatially  
85 complex and interconnected nature of river landscapes (hereafter riverscapes encompassing  
86 drainage channel networks, riparian zones and floodplains) means that a purely terrestrial or  
87 aquatic focus is inadequate.

88

## 89 **Methods**

90 We used hydrometric data to characterize the rhythmicity of flood regimes in a set of  
91 large river basins. Because biodiversity is known to peak at low latitudes (Willig et al. 2003), we  
92 chose rivers that had some portion or all of their catchment located in the tropics to minimize the

93 effects of latitude on ecosystem pattern and process. We accessed long-term daily discharge  
94 records from the Global Runoff Data Centre (GRDC,  
95 [http://www.bafg.de/GRDC/EN/Home/homepage\\_node.html](http://www.bafg.de/GRDC/EN/Home/homepage_node.html)), and limited our analyses to gauges  
96 with more than 20 years of data. We focused our efforts on gauges located in South America,  
97 Mexico and northern Australia where river regulation by dams and human-altered land cover are  
98 comparatively low, and the confounding influence of recent glaciation is absent. From these we  
99 selected those with upstream contributing areas greater than 10,000 km<sup>2</sup> (90 gauges in total;  
100 Figure S1), thus ensuring that the basin contained a significant floodplain (by surface area)  
101 (Tockner and Stanford 2002).

102         The area of floodplain subject to seasonal inundation is well correlated with river stage  
103 and discharge (Figure S2); therefore, we used daily discharge data from in-channel gauges to  
104 calculate summary metrics of the flood regime. Given the redundancy in many flow metrics, we  
105 selected two that describe the hydrologic rhythmicity of large river floodplains: the coefficient  
106 of variation (%) of the maximum annual flood peak ( $CV_{\text{maxann}}$ ) to describe variation in flood  
107 magnitude; and, the circular variance, a measure of the spread associated with a circular mean  
108 (the day of year of the maximum annual flood peak;  $PRED_{\text{timing}}$ ) to describe variation in flood  
109 timing. A perfectly rhythmic floodplain would receive a flood peak of identical magnitude  
110 ( $CV_{\text{maxann}} = 0$ ) on exactly the same day every year ( $PRED_{\text{timing}} = 0$ ), whereas a perfectly  
111 arrhythmic floodplain effectively exhibits random flooding, with a flood of any given size  
112 possible at any time of year.

113         Our selected river basins likely cover most of the global range in rhythmicity because  
114 Australian dryland rivers are known to be among the most temporally variable in the world  
115 (Puckridge et al. 1998) and large Amazonian tributaries have relatively low interannual variation

116 in flood timing and magnitude. We ranked the  $CV_{\text{maxann}}$  and  $\text{PRED}_{\text{timing}}$  of the 90 discharge  
117 gauges and used average rank ('rhythm rank score') as an overall indicator of rhythmicity, with  
118 scores close to one indicating rhythmicity and scores close to 90 indicating arrhythmicity. Our  
119 measure of interannual variation in flood magnitude ( $CV_{\text{maxann}}$ ) was correlated ( $r = 0.57$ ) with a  
120 seasonality index (percentage contribution of the six driest months of the year to total annual  
121 discharge) (Fig. S3), and thus it incorporates elements of both the low and high flow regime  
122 (Sabo and Post 2008).

123 We compared our rhythm rank scores with a set of biological features of tropical  
124 riverscapes that should be influenced by hydrologic rhythmicity and for which data were  
125 available. These included primary productivity of floodplain forests (terrestrial-process), export  
126 of dissolved organic carbon (DOC, aquatic-process), avian species richness and population  
127 variability (terrestrial-pattern) and fish species richness (aquatic-pattern).

128 We used rates of riparian forest production to indicate how river rhythmicity influences  
129 ecosystem processes in terrestrial areas. We estimated net primary productivity (NPP) of  
130 floodplain forests using modelled values from a global database (Kucharik et al. 2000). We used  
131 a valley bottom flatness index (Gallant and Dowling 2003) combined with images of remotely  
132 sensed inundation (Melack and Hess 2010) to obtain an objective estimate of floodplain area  
133 (independent of vegetation) and extracted NPP for delineated floodplains from an online  
134 database (Kucharik et al. 2000). Though we were unable to validate this approach with on-  
135 ground data for the Australian basins, we compared the model-derived estimate with on-ground  
136 measurements made in the central Amazon (Junk 1997) and found good agreement (model  
137 estimate ca.  $913 \text{ Mg C km}^{-2} \text{ yr}^{-1}$ ; on-ground estimate 800 to  $1250 \text{ Mg C km}^{-2} \text{ yr}^{-1}$ , Junk 1997).

138 Basin-scale data for aquatic ecosystem processes are scarce. One measure, catchment  
139 export of dissolved organic carbon (DOC), was available for six South American basins (collated  
140 in Aitkenhead and McDowell 2000) and two Australian basins (Daly River, Robson et al. 2010;  
141 Cooper Creek, S. Hamilton, unpublished data). Data for the South American basins and the Daly  
142 River are calculated based on measurements made across a range of flow conditions, while the  
143 Cooper Creek data are estimated from samples collected during low flows only. We used this as  
144 an approximate indicator of controls by rhythmicity on aquatic carbon flux.

145 To index response of riparian terrestrial biota to flood rhythmicity, data were compiled  
146 from a database of bird species observations from Australian basins maintained by BirdLife  
147 Australia (<http://birdlife.org.au/projects/atlas-and-birdata>). We calculated species richness in  
148 each basin as well as two standard measures of population variability, the standard deviation of  
149 log counts and the CV of abundance, for a subset of species with available data (present in  $n \geq 8$   
150 basins) that potentially respond to flood regimes because they depend on water or riparian  
151 corridors for feeding, nesting and refuge. These latter values incorporated both temporal and  
152 spatial variability in abundance within catchments, and thus can be considered measures of the  
153 repeated expansion and contraction of populations.

154 Our “aquatic pattern” indicator was fish species richness because fish play important and  
155 varied trophic roles in tropical rivers. We used data presented in Pusey et al. (2011) for northern  
156 Australian basins and in Albert et al. (2011) for South American basins. Data presented in Pusey  
157 et al. (2011) were based on museum records, published survey accounts and unpublished survey  
158 data (Pusey, Kennard and Burrows, unpublished data) for almost 7000 sites throughout northern  
159 Australia. These data form a significant component of the most recent assessment of the  
160 conservation value of aquatic ecosystems of the region (Kennard et al. 2010). Recognizing the

161 limitations in accurately assessing species diversity for South America, a large and incompletely  
162 inventoried region (Alofs et al. 2014), we used fish river basin species richness from Albert et al.  
163 (2011), which currently provides the most comprehensive assessment based on ~5600  
164 Neotropical species.

165 For all analyses, we log-transformed response data, where appropriate, and used simple  
166 linear or exponential regressions to test for relationships between rhythm rank scores and  
167 biological characteristics using SPSS (SPSS Inc, Chicago, IL). Because larger basins are known  
168 to contain more diverse assemblages (Guégan et al. 1998), we scaled all fish diversity measures  
169 to basin size by dividing by catchment area. Similarly, we report both floodplain NPP and DOC  
170 export on a per-unit-area basis, thus removing the potential confounding effect of river size.

171

## 172 **Results**

173 Our rhythm framework shows that there are large differences within and among the two  
174 study regions in the predictability of the magnitude and timing of floods (Fig. 1). Between  
175 regions, differences are most pronounced for interannual variation in flood magnitude  
176 ( $CV_{\maxann}$ ), whereas predictability of flood timing ( $PRED_{\text{timing}}$ ) is more comparable between the  
177 two regions (Fig. 1A). Floods in Australian rivers are generally less rhythmic than those in  
178 South American and Mexican systems (Fig. 1B). Australian rivers rank between 64<sup>th</sup> (Daly  
179 River) and 90<sup>th</sup> (Cooper Creek) out of the 90 basins in  $CV_{\maxann}$  (ranging from 61 to 197%), and  
180 South American and Mexican rivers had  $CV_{\maxann}$  ranging from 4 to 131% and ranking from 1<sup>st</sup>  
181 (Rio Purus) to 87<sup>th</sup> (Rio Bana Buiú). Temporal variation in Australian rivers reflects the climatic  
182 range from the more predictable monsoonal tropics (e.g., Daly River,  $PRED_{\text{timing}} = 0.08$ , rank =  
183 14) to less predictable dryland rivers draining the continent's interior (e.g., Cooper Creek,

184  $PRED_{\text{timing}} = 0.55$ , rank = 80). South American rivers varied in  $PRED_{\text{timing}}$  from 0.02 in the  
185 Orinoco River (rank = 1) to 0.93 in the Rio Ivaí (rank = 90), the latter lacking a distinct rainy  
186 season that leads to floods throughout the year (Fig. 1C).

187         Analysis of structural and functional features of aquatic and terrestrial riverscape  
188 components revealed that ecological responses to flood rhythmicity vary in direction, form and  
189 strength. For example, variation in floodplain forest annual NPP is negatively related to rhythm  
190 rank score for the Australian river basins ( $r^2 = 0.42$ ,  $p = 0.007$ , Fig. 2A). The analysis also  
191 suggests possible links between rhythmicity and export of dissolved organic carbon (DOC)  
192 across all rivers ( $r^2 = 0.54$ ,  $p = 0.037$ , Fig. 2B). Australian bird species richness is related to  
193 rhythmicity ( $r^2 = 0.35$ ,  $p = 0.043$ , data not shown), and when examined for particular functional  
194 and taxonomic groups, correlations between rhythm rank score and measures of population  
195 variation (SD of log counts and CV) were almost uniformly positive (Fig. 2C), suggesting that  
196 less rhythmic rivers have more variable avian populations. A significant amount of variation in  
197 fish species richness was explained by the flood rhythm of the Australian basins ( $r^2 = 0.54$ ,  $p =$   
198  $0.006$ ) and for the two regions combined ( $r^2 = 0.43$ ,  $p = 0.001$ ), but not for the South American  
199 basins alone ( $r^2 = 0.01$ ,  $p = 0.795$ , Fig. 2D).

200

## 201 **Discussion**

202         These results reveal the broad range of hydrological rhythms and ecological responses in  
203 floodplain riverscapes of two tropical regions. Fish and bird species assemblages and two  
204 important ecosystem processes respond to this gradient. Fish species richness is higher, avian  
205 populations are more stable, and forests are more productive when river flow is more rhythmic.  
206 Aquatic primary and secondary production is stimulated when seasonal warm temperatures and

207 sustained flood pulses are synchronized (Winemiller 2004). In contrast to the wet tropics where  
208 river flow pulses tend to be rhythmic, rivers in semi-arid to arid climates generally have  
209 arrhythmic discharge (Fig. S1) associated with low mean annual runoff (Fig. S4A). Despite  
210 having daily flood peaks that rival and often exceed those of rhythmic rivers (Fig. S4B),  
211 arrhythmic rivers have floodplains dominated by sparse catchment vegetation (Fig. 3A) and  
212 limited export of DOC (Fig. 3B). Birds in arrhythmic rivers show variable population  
213 abundances (Fig. 3C) with ‘boom and bust cycles’ that likely reflect their well-known ability to  
214 disperse and track surface water availability (Kingsford and Norman 2002). Such arrhythmic  
215 rivers support opportunistic fish species that are tolerant to high temperatures, low oxygen and  
216 high turbidity that are often associated with no-flow conditions (Sabo et al. 2010). More  
217 rhythmic rivers support a greater number of species that require access to permanent floodplain  
218 wetland habitats (Fig. 3D, Lewis et al. 2000) and provide a greater flood pulse advantage for  
219 aquatic consumers. This latter feature is frequently revealed by a disconnect between the stable  
220 isotopic signatures of fish and local food resources in channel habitats of rivers that experience  
221 extensive and relatively predictable flood pulses (Fig. S5). Many other ecological processes  
222 such as secondary productivity and nutrient release rates from sediments and soils (Bechtold et  
223 al. 2003), as well as important interactions among producers, grazers and predators (Power et al.  
224 2008), are affected by hydrologic rhythmicity.

225         In theory, harsh and fluctuating environments limit diversity in biological communities.  
226 The relative abundances of two competing species are determined by differences in their ratios  
227 ( $E/b$ ) of average environmental response ( $E$ ) to sensitivity to competition ( $b$ ) (Chesson and  
228 Huntly 1997). Under a scenario of regular but predictable disturbance (e.g. high flood  
229 rhythmicity), extinction probabilities do not increase because disturbance ‘averages out’ over

230 time and competitively inferior species exhibit positive growth rates at low densities, an  
231 important criterion for stable coexistence (Gravel et al. 2011). Further, predictable disturbances,  
232 such as rhythmic floods, would allow a larger suite of organisms to maintain viable populations  
233 via storage effects, or to persist during unfavorable conditions (Chesson et al. 2004). Hence,  
234 though rhythmic rivers could be described as harsh, fluctuating environments, their relatively  
235 predictable fluctuations may promote more diverse and productive communities (Chesson and  
236 Huntly 1997). Under stochastic disturbance or non-stationarity (e.g. a new flow regime  
237 introduced by a dam), local extinctions are instead hastened by competitive exclusion or random  
238 drift (Chesson and Huntly 1997). Many arrhythmic rivers experience occasional periods of  
239 drought and no flow which represents a second type of disturbance. Harsh drought conditions  
240 reduce critical resources and populations of aquatic organisms, but are eventually followed by  
241 rapid population growth when flows are reestablished (Burford et al. 2008) and a return to  
242 intense competition until the next disturbance event.

243         Differences in diversity between rhythmic and arrhythmic rivers are consistent with the  
244 Intermediate Disturbance Hypothesis (IDH) that predicts peaks in species diversity at  
245 intermediate levels of disturbance. Since the development of the IDH, a variety of diversity vs.  
246 disturbance relationships have been observed (Mackey and Currie 2001) that likely arises from  
247 difficulties in characterizing and measuring disturbance (Shea et al. 2004). Though aspects of  
248 disturbance normally considered include frequency, extent, intensity and duration, only recently  
249 has clarity emerged around the simultaneous characterization of disturbance in multiple  
250 dimensions (Miller et al. 2011). While variation is implicit in all of these aspects, predictability  
251 of the disturbance may be as important as its magnitude.

252 Our rhythm framework characterizes disturbance as regular and predictable vs. irregular  
253 and unpredictable, and our two-dimensional rhythm rank scores can be examined as sample  
254 distributions for each component variable (Figure S6, c.f. Miller et al. 2011). These event  
255 distributions show a more normal distribution of intensity and frequency for highly rhythmic  
256 systems and a dispersed, right-skewed distribution for frequency and intensity for highly  
257 arrhythmic systems. Thus, within a given arrhythmic system, the interval between floods is  
258 always too long and flood size is too small, favoring few strong competitors, or the interval is too  
259 short and flood size is too large, favoring few tolerant species. More rhythmic systems,  
260 conversely, are subject to disturbance that is intermediate in both frequency and intensity.  
261 Arrhythmicity also increases the likelihood that a flood pulse will occur during cooler months  
262 with a reduced photoperiod, and thus outside the optimal period for growth. These aseasonal  
263 flood pulses are likely to limit, rather than enhance, diversity and production (Winemiller 2004),  
264 much like the arrhythmic rivers shown here.

265 If our reasoning is correct, then neutral models of species diversity (e.g. Muneeppeerakul  
266 et al. 2008) should predict better for regions with less rhythmic rivers, because rates of birth,  
267 death and immigration in response to the disturbance regime, rather than local niche partitioning,  
268 will most strongly influence assemblage structure. Given that predictability as a measure of  
269 disturbance has long been debated (e.g. Poff 1992), there is little doubt that seasonally  
270 predictable environments provide greater opportunities for specialized life-history adaptations  
271 than do unpredictable environments. This entails a necessary trade-off in the relative fitness  
272 benefits of particular life histories across gradients of predictability. The generalist diets and  
273 habitat use patterns of fishes in arrhythmic Australian rivers (Pusey et al. 2011) supports this  
274 assertion, whereas the highly diverse and ecologically specialized fishes of rhythmic South

275 American basins (Lewis et al. 2000, Correia and Winemiller 2014) suggests that deterministic  
276 models would better explain patterns of local species richness. Until more species distribution  
277 data become available for South American systems (Albert et al. 2011, Alofs et al. 2014) to  
278 allow testing of neutral models, this remains speculative. Higher fish diversity for a given  
279 rhythm rank score for South American basins compared to Australian basins (Fig. 1D) is likely a  
280 function of the former's greater regional species pool within a greater land area, and the latter's  
281 paleohistory of desertification that caused many species extinctions (Unmack 2001).

282 Latitude and local geomorphology also may have influenced ecological patterns and  
283 processes within and across the two regions. By constraining our analysis to tropical basins, our  
284 gauges covered a latitudinal range of 52 degrees (-29° to 22°). The Australian gauges, those  
285 having the strongest rhythmicity-diversity relationships, spanned a lesser latitudinal gradient (-  
286 27° to -14°). Diversity of many higher taxa peaks at these tropical latitudes, and significant  
287 diversity-latitude relationships are uncommon across such a narrow range (Willig et al. 2003).  
288 Expansion of our framework to include other regions should consider latitude as a potential  
289 covariable. Channel and floodplain geomorphology also strongly influence patterns of nutrient  
290 retention and transformation (Noe et al. 2013); thus, biological diversity and productivity in both  
291 rhythmic and arrhythmic rivers are likely modulated by the landforms through which they flow  
292 (hydrogeomorphic patches *sensu* Thorp et al. 2008).

293 Our analysis implies potential negative consequences from intensification of the  
294 hydrological cycle that has been projected in response to global climate change. Intensification  
295 that leads to more extreme rainfall-runoff events (Palmer et al. 2008) will alter the timing and  
296 magnitude of flood peaks. In these regions, rivers will be pushed toward the arrhythmic end of  
297 the spectrum (Döll and Zhang 2010), potentially reducing deterministic influences on

298 populations and communities (Lewis et al. 2000, Clark 2008), and increasing stochastic  
299 influences (Sabo and Post 2008, Rosindell et al. 2012). Ecological responses to altered thermal  
300 and precipitation regimes and increased frequency of extreme climatic events have already been  
301 observed, including changes in the timing of bird migrations, variable survival of offspring, and  
302 mismatches between consumers and prey as well as seed production and pollinators (Helm et al.  
303 2013). Rapid change that alters interannual variation in magnitude and timing of seasonal  
304 inundation could shift communities away from species better adapted to exploit predictable flow  
305 pulses towards those more tolerant of unpredictable flow pulses that have bet-hedging life-  
306 history traits such as asynchronous reproduction (Lytle and Poff 2004).

307         In the near term, effects of altered river hydrology derived from climate change may pale  
308 in comparison to more immediate hydrological modifications from dams for hydroelectric power  
309 generation, water storage and water diversion for agriculture, industry and urban areas (Palmer et  
310 al. 2008). The rhythmicity framework presented here can be used to consider how river  
311 regulation and water extraction may affect the important ecosystem services provided by large  
312 river floodplains, and how the management of dams interacts with climate-driven changes to  
313 alter runoff characteristics (Palmer et al. 2008, Fig. S4A).

314         Our analysis has implications for the restoration of flood-dependent ecosystems in large  
315 rivers where prescribed floods are being used to trigger desired geomorphological and biological  
316 responses (Olden et al. 2014). For example, single rare floods, such as those used in the Colorado  
317 River (USA) to rebuild sandbars and other in-stream habitats, may not meet other ecological  
318 objectives (Cross et al. 2011). A single large flow pulse can effectively move bed materials and  
319 create backwater habitat; however, flow pulses must occur with sufficient rhythmicity to allow  
320 locally-adapted organisms to thrive in the face of competition from non-natives (Cross et al.

2011). Repeated floods that mimic the timing and magnitude of pre-development conditions (Robinson and Uehlinger 2008) are required for river-floodplain systems to return to a state that approximates the original distribution of species and their abundances (Poff et al. 2007). Analysis of flow pulse rhythmicity before and after dam construction could assist in prescribing long-term strategies required to restore key functions and structures of river ecosystems.

Relationships between rhythmicity and species diversity, population variation and riparian primary productivity, coupled with the prior observation that high variation in discharge limits food chain length in rivers (Sabo et al. 2010), lend further support to the idea that hydrological predictability is a key driver of ecological patterns and processes in riverine landscapes. Much like the predictable arrival of spring heralds an oncoming peak in growth and reproduction for biota, so too does the rhythmicity of large rivers support productive and diverse life forms that generate ecosystem services for human societies.

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478 **Figure legends**

479 **Figure 1** The rhythmicity of river floodplains in South America and Mexico (green squares) and

480 Australia (orange diamonds), as indicated by summary metrics of the long-term flood regime.

481 (A) A gradient of rhythmicity (indicated by the arrow) distinguishes floodplains ranked on the

482 basis of predictability in timing (y axis,  $PRED_{\text{timing}}$ ) and interannual variation in the maximum

483 flood peak (x axis,  $CV_{\text{maxann}}$ ). (B) Frequency histogram of rhythm rank scores for the two main

484 regions. (C) Examples of monthly discharge hydrographs of representative floodplains. The five

485 example rivers, from top to bottom, are from western Australia, southern Brazil, north-central

486 Australia, and the eastern and western Amazon in Brazil.

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488 **Figure 2** Relationship between riparian forest production (A), dissolved organic carbon export

489 (B), avian population variability (C), and fish species richness (D) and hydrological rhythms of

490 tropical rivers (rhythm rank score). Rhythm rank score is the average rank from Figure 1. In

491 panel (C), correlation coefficients ( $r$ ) denote species-specific responses in population CV (y-axis)

492 and the logarithm of species counts (x-axis) to rhythm rank score (i.e. a positive  $r$  implies greater

493 population variability associated with a higher rhythm rank score).

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495 **Figure 3** A) Defoliated and damaged vegetation along the arrhythmic Flinders River, Australia

496 after recession of an extended flood in the Austral summer of 2009. Floods of similar duration

497 that occur annually in the Amazon lead to high productivity because of local adaptations of tree

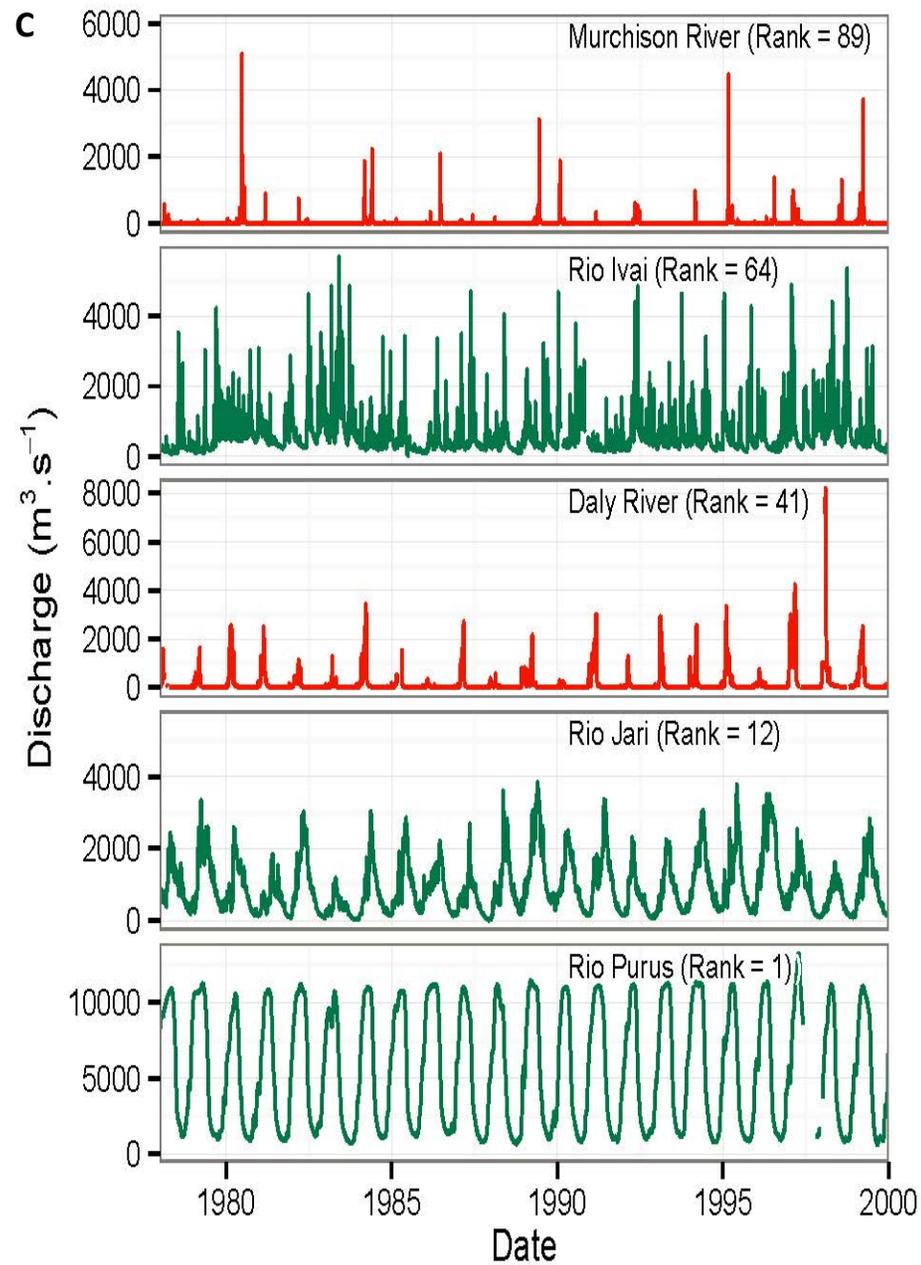
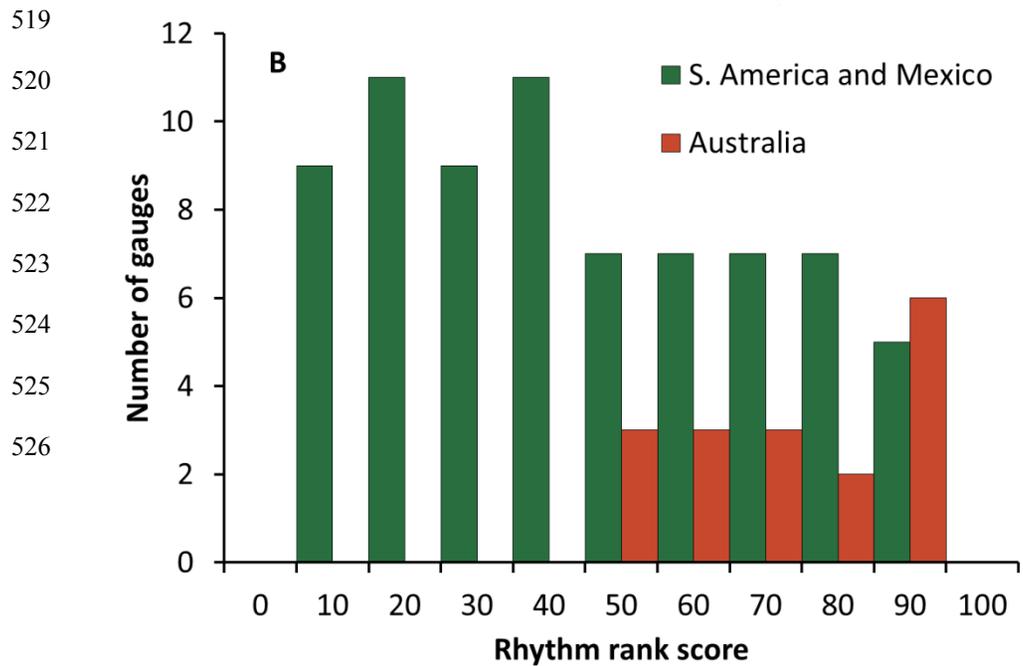
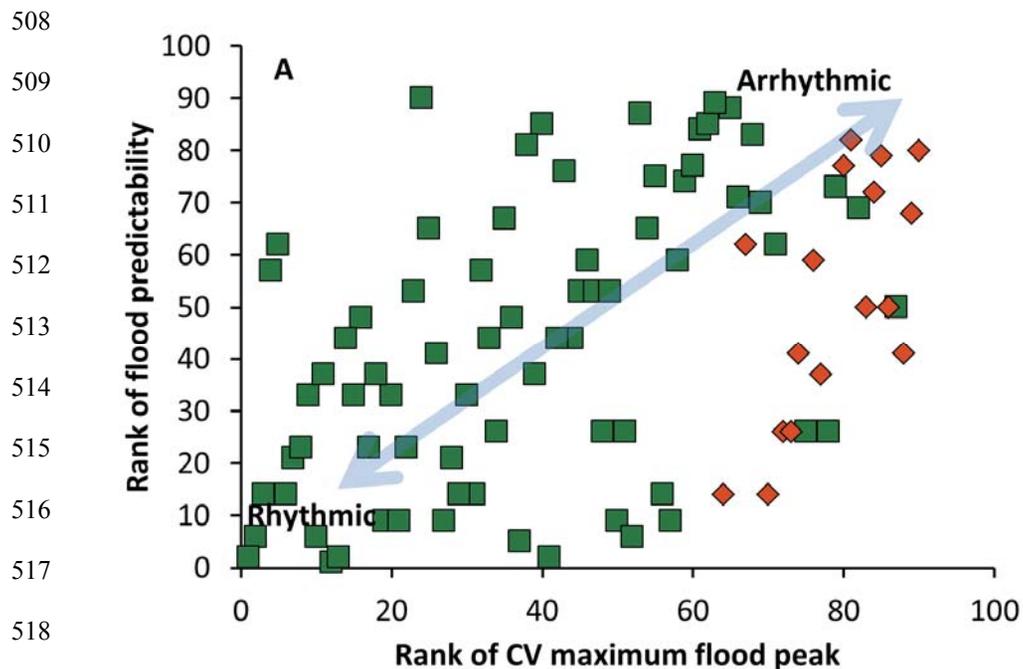
498 species to submergence and anoxia. Photo credit: Stephen Hamilton. B) The floodplain of the

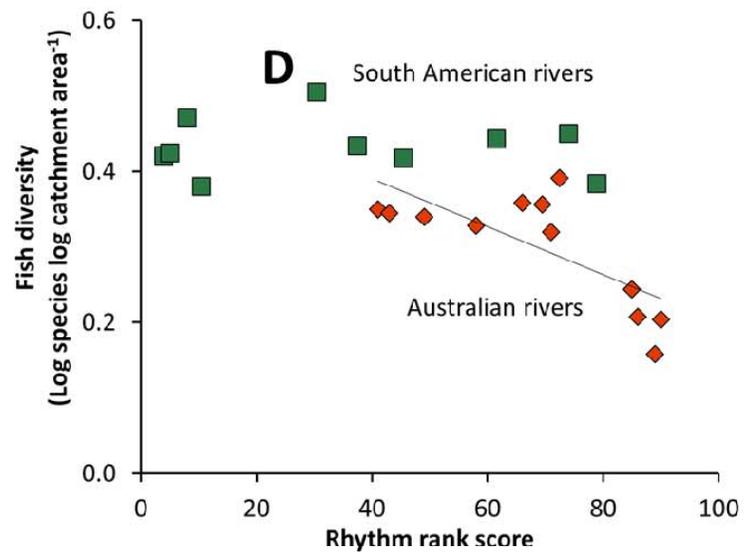
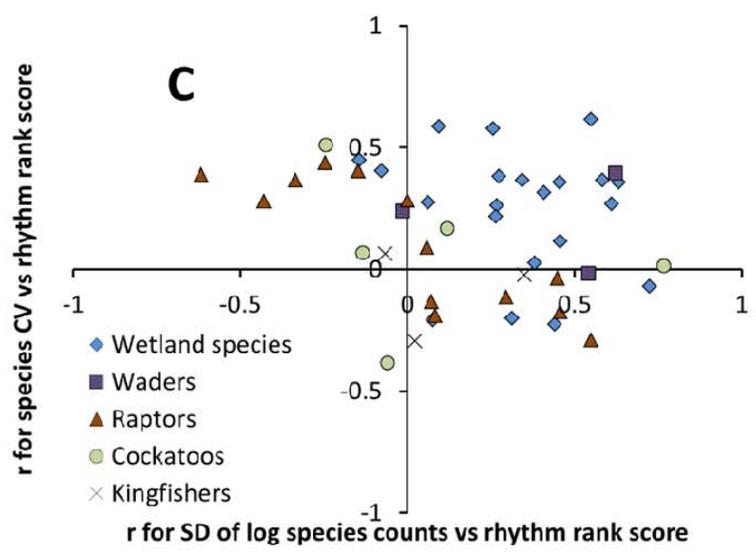
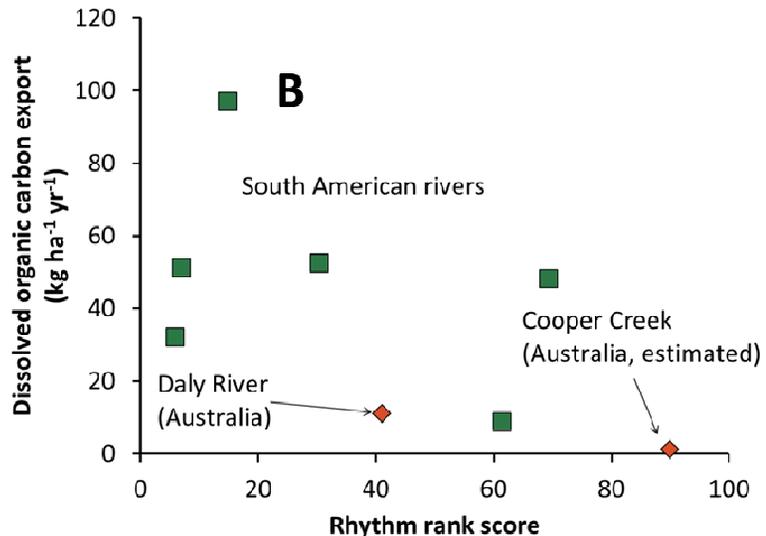
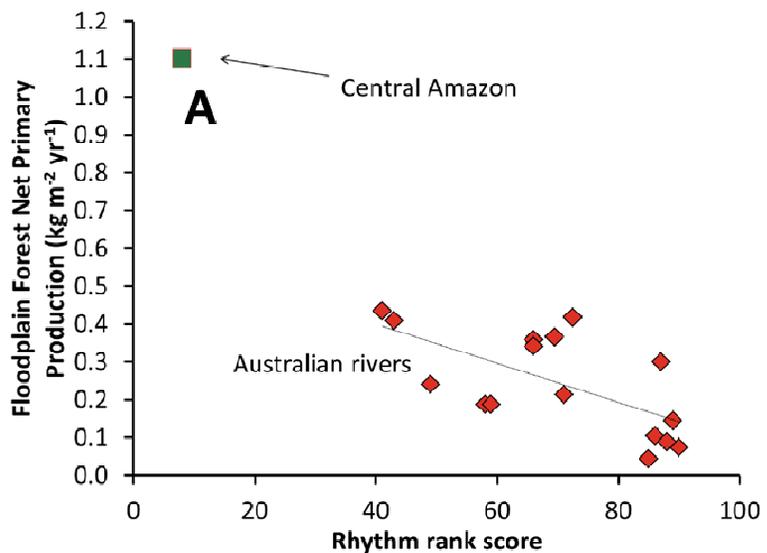
499 Napo River, an Amazonian tributary in Ecuador, often has waters rich in dissolved organic

500 carbon. Photo credit: Kateryna Rybachuk. C) Pelicans in a floodplain waterhole of the Mitchell

501 River, Australia. Highly variable avian populations occur commonly in arrhythmic rivers. Photo  
502 credit: Tim Jardine. D) Some of the fish species that are common in the most rhythmic  
503 Australian rivers (clockwise from top left: Lake grunter *Variichthys lacustris*, Pennyfish –  
504 *Denarius bandata*, Saratoga – *Scleropages jardinii*, Delicate blue eye – *Pseudomugil tenellus*  
505 (images by Neil Armstrong).  
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507 **Figure 1**





529 **Figure 3**

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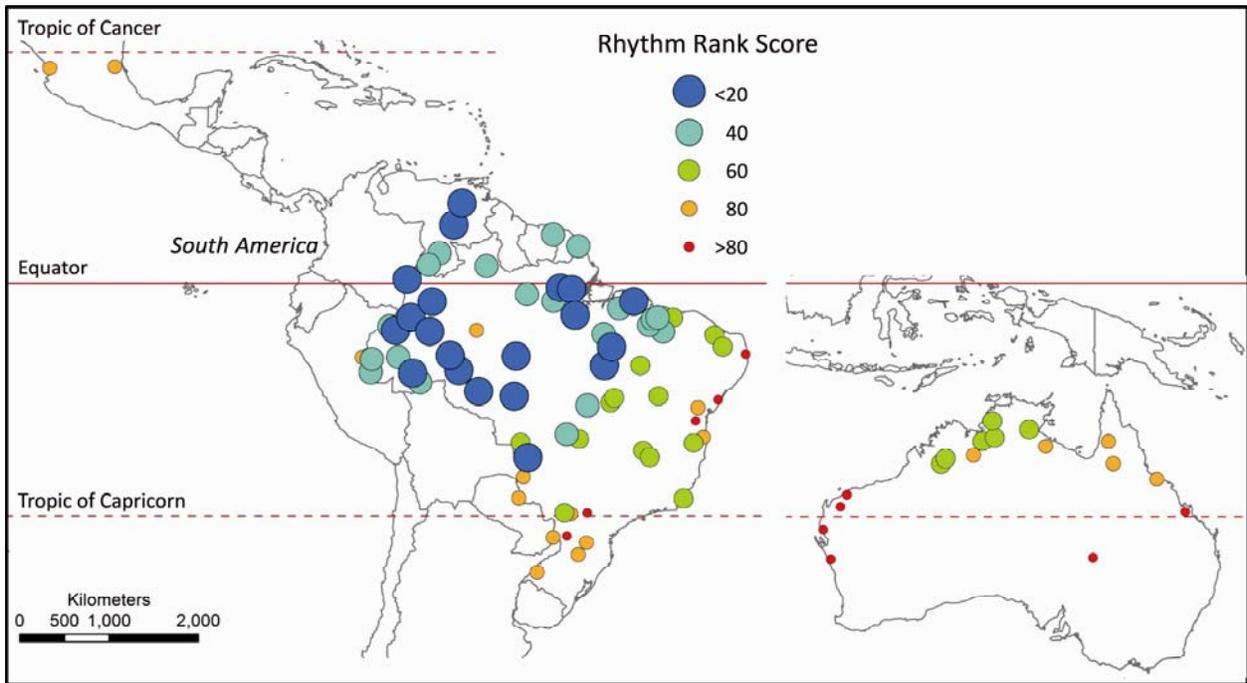
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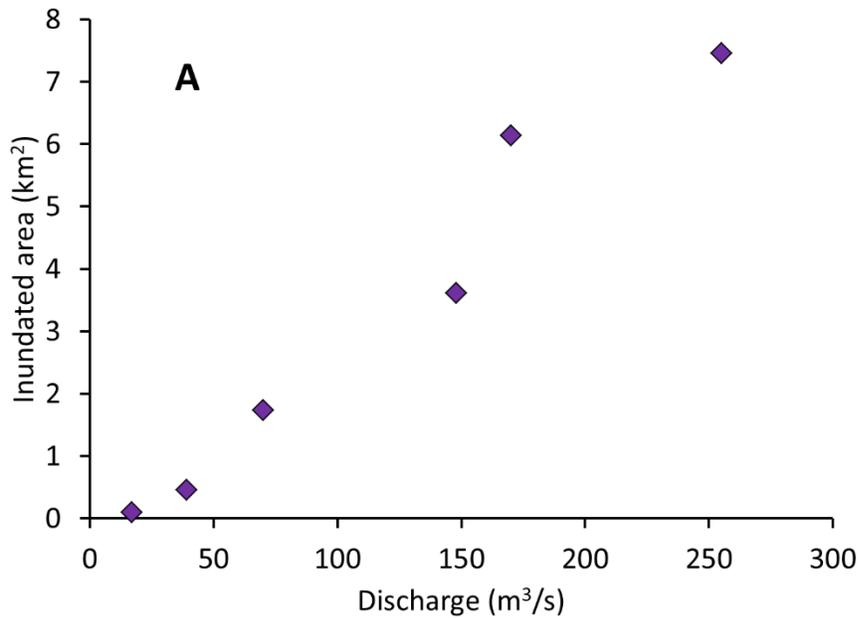


1 **Figure S1** Gauge locations and corresponding rhythm rank scores for the river basins included  
2 the study. Rhythm rank scores scale from most rhythmic (low variability in flood magnitude and  
3 timing among years, ranks <20, large blue bubbles) to most arrhythmic (high variability in flood  
4 magnitude and timing, ranks >80, small red bubbles).

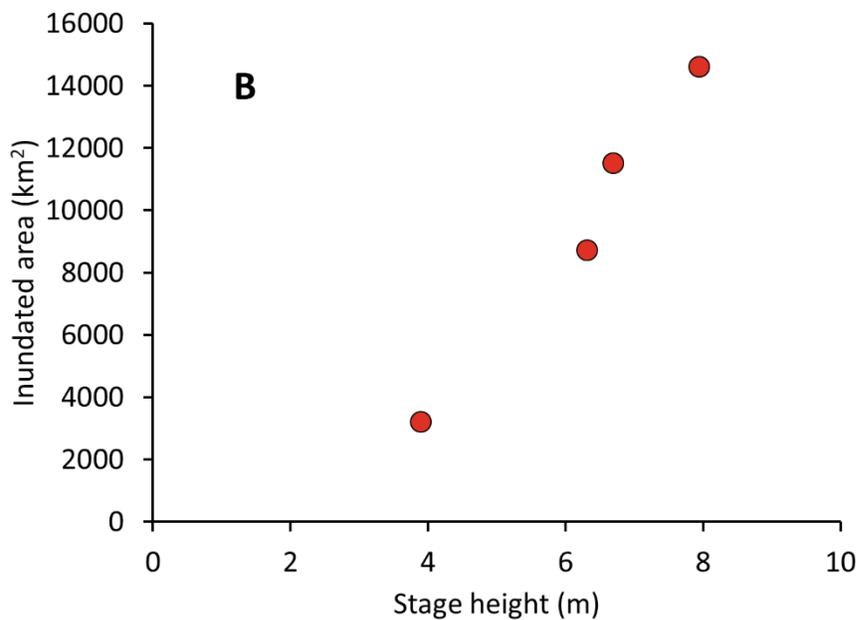


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24 **Figure S2** Examples of correlations between in-stream gauge readings and floodplain  
25 inundation: (A) discharge ( $\text{m}^3/\text{s}$ ) vs. inundated area ( $\text{km}^2$ ) from the Ogeechee River, USA  
26 (adapted from Benke et al. 2000); (B) stage height (m) vs. inundated area ( $\text{km}^2$ ) for Cooper  
27 Creek, Australia (adapted from Cobon and Toombs 2007). See also Hamilton et al. (2002) for  
28 several South American examples.



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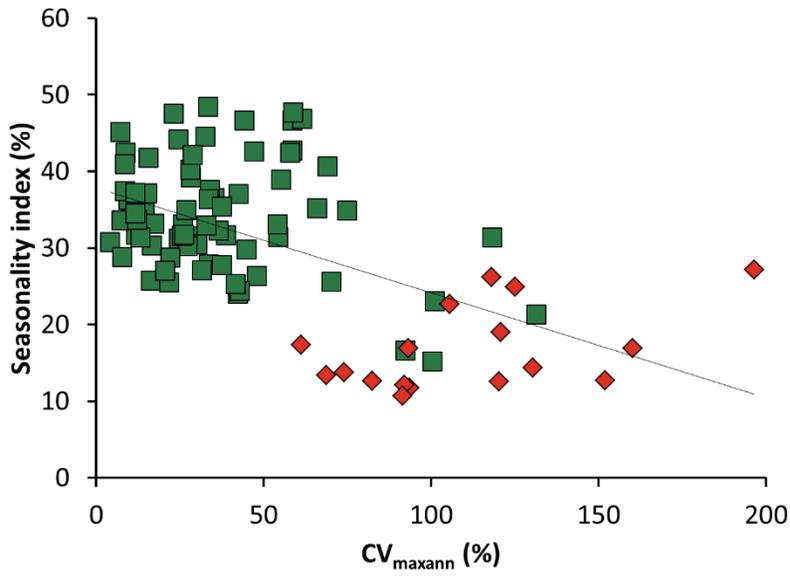
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53 **Figure S3** Seasonality index (% of annual discharge from the six driest months of the year) vs.  
54 interannual variation in the maximum flood peak ( $CV_{\maxann}$ , %) for floodplain rivers in South  
55 America and Mexico (green squares) and Australia (orange diamonds).



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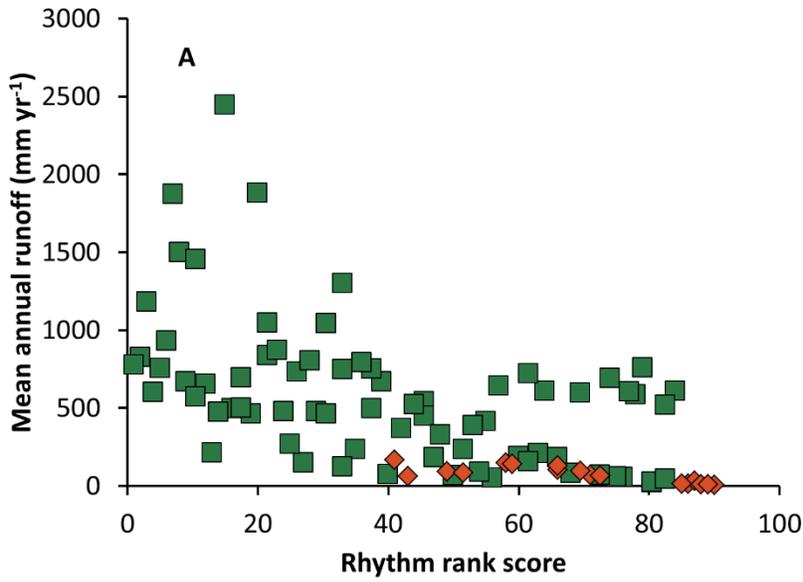
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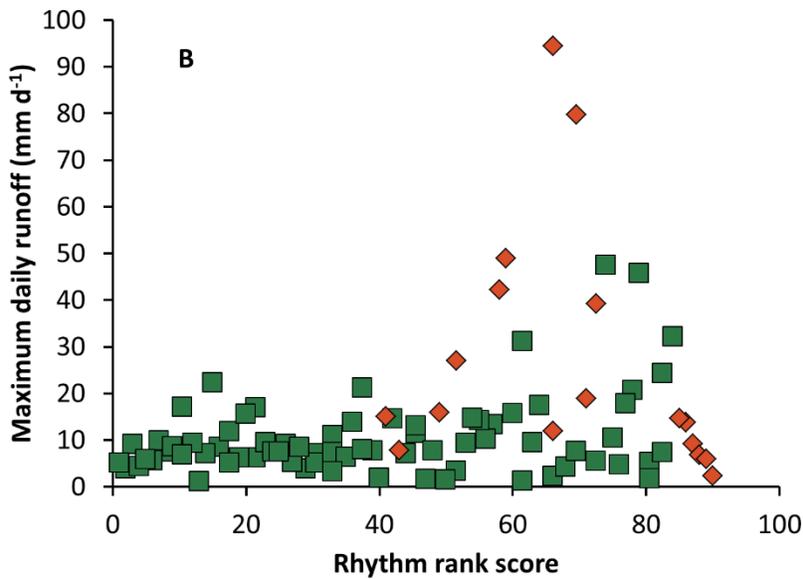
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67 **Figure S4** Mean annual runoff (A, mm yr<sup>-1</sup>) and maximum daily runoff (B, mm day<sup>-1</sup>) vs.  
68 rhythm rank scores for floodplain rivers in South America and Mexico (green squares) and  
69 Australia (orange diamonds).

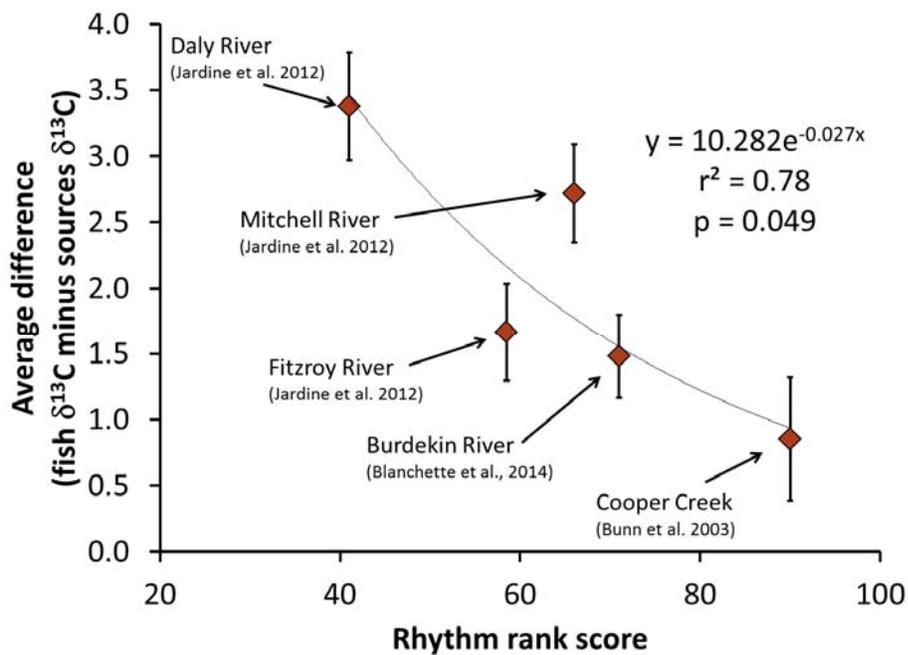


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80 **Figure S5** The average difference in stable isotope ratios ( $^{13}\text{C}/^{12}\text{C}$ ) of carbon ( $\delta^{13}\text{C}$ ) between fish  
81 and local food sources (benthic invertebrates and periphyton) collected from multiple locations  
82 in rivers that vary in rhythmicity. More rhythmic rivers contain fish that have derived their body  
83 mass from outside the location of capture (i.e. predictably available floodplains), whereas the  
84  $\delta^{13}\text{C}$  of fish from arrhythmic rivers are closely aligned with local prey, indicating local foraging.



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**Figure S6** Frequency histograms of inter-flood interval (A, days) and maximum annual flow (B,  $\text{m}^3 \text{s}^{-1}$ ) for representative rivers from South America (green) and Australia (orange), with corresponding rhythm rank scores (see methods). Inter-flood interval was calculated as the number of days between events that exceeded the upper 80th percentile of flows for the record.

