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#### Supporting Online Material

www.sciencemag.org/cgi/content/full/330/6006/957/DC1 Material and Methods Figs. S1 to S14 Tables S1 to S10

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## Conditional Cooperation and Costly Monitoring Explain Success in Forest Commons Management

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Recent evidence suggests that prosocial behaviors like conditional cooperation and costly norm enforcement can stabilize large-scale cooperation for commons management. However, field evidence on the extent to which variation in these behaviors among actual commons users accounts for natural commons outcomes is altogether missing. Here, we combine experimental measures of conditional cooperation and survey measures on costly monitoring among 49 forest user groups in Ethiopia with measures of natural forest commons outcomes to show that (i) groups vary in conditional cooperator share, (ii) groups with larger conditional cooperator share are more successful in forest commons management, and (iii) costly monitoring is a key instrument with which conditional cooperators enforce cooperation. Our findings are consistent with models of gene-culture coevolution on human cooperation and provide external validity to laboratory experiments on social dilemmas.

aintaining large-scale cooperation for the provision of public goods and the management of common property is fraught with the infamous cooperation dilemma in which free riders enjoy group benefits without bearing the cost of their provision. The conventional analysis, based on the assumption of selfregarding individuals, predicts zero cooperation under these conditions (1, 2). Yet extensive field evidence underlines that many groups are able to manage their commons, albeit with varying degrees of success (3, 4). This marked deviation from the conventional hypothesis as well as the variation in management success necessitates a coherent theory of human collective behavior that explains well the observed variation in cooperation outcomes. In addition to structural factors like resource characteristics, group size, and socioeconomic heterogeneity (3–5), recent findings suggest that social behaviors, such as the norm of conditional cooperation (individual cooperation being conditional on the cooperation of others) together with the costly enforcement of this norm, may play an important role in stabilizing large-scale cooperation (6-8).

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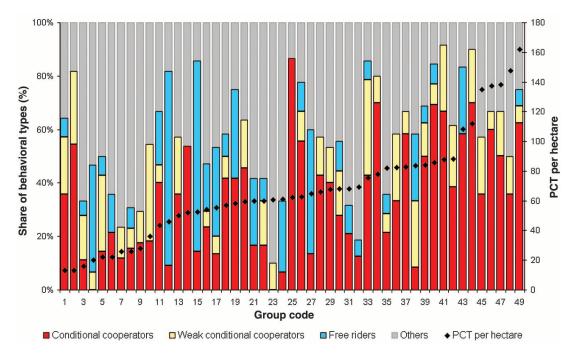
Much of the evidence for conditional cooperation comes from behavioral laboratory experiments with student participants showing that individuals display a considerable heterogeneity in their behavioral disposition to cooperate. Although a large proportion of participants reveal conditionally cooperative behavior, a nontrivial share meets the conventional assumption by behaving as free riders (9-14). Because conditional cooperators do not cooperate if many group members ride for free, the composition of a group becomes decisive for the prospects of maintaining cooperation. Whereas voluntary cooperation may be achieved in groups with larger share of conditional cooperators (15, 16), in heterogeneous groups costly norm enforcement is needed to attain cooperation (6, 17–21). Evidence shows that many individuals, in particular those with a high propensity to cooperate, are willing to enforce cooperation even at a personal cost (17, 22-26) and that this has a positive effect on group members' contribution (17, 19, 27, 28).

The large body of evidence for conditional cooperation and costly norm enforcement is compelling. However, unless the relations between these behaviors and the way they affect outcomes of commons management are investigated in a concrete field setting, where one can account for context-specific information regarding relevant structural factors, their ultimate impact for commons management is hard to evaluate (29–31). Although previous studies have conducted be-

havioral experiments with diverse populations including commons users (26, 32-36) and have tentatively documented the importance of local enforcement in the field (21, 37), reliable evidence on the extent to which variation in conditional cooperation and costly norm enforcement among commons users affects natural commons outcomes is altogether missing.

We combined data on natural outcomes of commons management with experimental measures of conditional cooperation among 679 individuals from 49 commons user groups to investigate whether groups with larger share of conditional cooperators achieve better outcomes (38). We also measured costly enforcement through survey data on monitoring, an important input for the detection and punishment of free riding in our context, to analyze the extent to which monitoring plays a role in sustaining commons outcomes by conditional cooperators. In doing so, we aimed to underline the conditions under which local enforcement of commons management is predicted to work.

Our research strategy was to carry out these investigations in a field setting where individuals in a group face a natural commons dilemma and use costly enforcement mechanisms to overcome this dilemma and where there exists a reliable measure of cooperation outcomes in commons management. We conducted our study in the context of a major forest commons management program launched to save local forests and livelihoods in the Bale region of Ethiopia. Under the program, groups of the Bale Oromo people were given secure tenure rights to use and manage their forests as common property resources (39). In return, these groups are required to maintain their forest cover, for which they are allowed to implement local rules regarding forest use, for instance, the amount of fuelwood a member is allowed to harvest for self-consumption and sale. While managing their forest as a common property, group members confront cooperation dilemmas, because each member is better off when every member in the group cooperates by adhering to internal rules; however, violating the rules leads to higher payoffs, for instance, from the sale of extra fuelwood, implying that individual members might have little incentive to cooperate. To overcome this first-order dilemma, members have the option to engage in costly monitoring, which involves conducting patrols through the forest. Such patrols not only deter



**Fig. 1.** Forest management outcome as measured in potential crop trees (PCT) per hectare and the relative shares of the main behavioral types in a group. The groups are sorted by PCT. Each bar represents a group engaged in the management of forest commons identified by its numerical code. There is

large variation in the forest management outcome (min = 13, max = 161.9, SD = 35.2) and in the share of conditional cooperators (min = 0%, max = 86.7%, SD = 21.5%) and free riders (min = 0%, max = 72.7%, SD = 17.2%) across groups.

free riding in itself but also generate information needed for the punishment of free riders, which is determined by an executive committee on the group level chaired by the group leader. Because forest patrols cost members time and effort but generate group benefits, they are associated with a second-order cooperation dilemma.

Data collected by the program office on the outcome of commons management for each group using mensuration data on potential crop trees (PCT) [supporting online material (SOM) text] exhibit tremendous variation (Fig. 1). Because inventory studies conducted before the launch of the program indicated no major variation in PCT (40), the large variation in current outcomes suggests that groups achieve different degrees of success in overcoming cooperation dilemmas in managing their commons. We hypothesize that groups with larger share of conditional cooperators are more likely to be successful at managing their commons and that they achieve this by using costly monitoring as a mechanism.

To test our hypothesis, we measuref conditional cooperation among commons users by using a public goods game as a stylized model of the cooperation dilemma associated with commons management. We followed the experimental protocol of (10), which controls for individuals' beliefs about the cooperation of others. Controlling for beliefs is important because by the very definition conditional cooperators will not cooperate if they believe that others will not cooperate. It is thus not possible, for example, to infer the absence of conditional cooperators from a group in which little cooperation is observed. Our experimental proto-

**Table 1.** Criteria for identifying behavioral types and their share in our sample. We follow (10) and use Spearman's  $\rho$  between a participant's and a partner player's contribution to elicit a participant's behavioral type. We classify a player as conditional cooperator if the Spearman's  $\rho$  is positive and significant at  $P \leq 0.001$ , weak conditional cooperator if the Spearman's  $\rho$  is positive and significant at 0.001 < P < 0.05, free rider if a player consistently contributes zero independent of the partner player's contribution or contributes at most the smallest positive amount in only one of the seven decisions, altruist if a player consistently contributes the entire endowment regardless of the partner's contribution, and hump-shaped if the contribution increases up to a point with the partner's contribution and then decreases (based on visual examination).

Behavioral type	N	º/o	Mean Spearman ρ	
Conditional cooperator	231	34.02	0.99	
Weak conditional cooperator	79	11.63	0.86	
Free rider	78	11.49	-0.08	
Hump-shaped	20	2.95	-0.04	
Altruist	15	2.21	0.00	
Other	256	37.70	0.15	
All players	679	100.00	0.48	

col enabled us to circumvent this problem, providing an explicit measure of conditional cooperation.

In the public goods game, two players from the same user group were randomly paired in a one-shot and anonymous interaction. Each of the two players received six bills of one Ethiopian Birr (the equivalent of a day's wage) and had to decide on his contribution to a public good, which was then multiplied by 1.5 and distributed equally among the two players irrespective of players' individual contributions. The game constitutes a cooperation dilemma because players together are best off if both contribute their entire endowment to the public good; however, because the individual cost of contributing one Birr to the public good is one but the return is only 0.75, each player's earning is max-

imized by contributing zero to the public good independent of the other player's contribution.

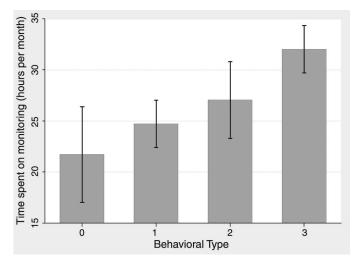
Players took two decisions in the experiment: an unconditional and a conditional decision. In the first decision, both players decided simultaneously on their contribution to the public good and stated the expected contribution of the partner player. The second decision was sequential in which players were visualized one by one each of the seven possible contribution decisions of their partner player and asked to state their own contribution to the public good for each of the other player's contributions. At the end of the experiment, a die was rolled to determine the player for whom the first decision was taken; this was matched with the second decision of the other player to deter-

**Table 2.** Forest management outcome, conditional cooperation, and structural variables. The dependent variable is forest management outcome, measured in PCT per hectare. The independent variables are conditional cooperator shares, market distance, and time. Additional controls include elevation, group size, share of female members, and heterogeneity in livestock ownership. Ordinary least squares (OLS) estimates with robust standard errors in parentheses. \*\*\*P < 0.01.

Dependent variable: Forest management outcome

Variables	1	2	
Conditional cooperator share		52.085*** (13.117)	
Market distance	<b>–22.779***</b> (4.355)	<b>-20.568***</b> (4.057)	
Time	36.479*** (6.409)	32.185*** (6.004)	
Constant	105.325*** (21.719)	81.438*** (19.186)	
Additional controls	Yes	Yes	
Adjusted r <sup>2</sup>	0.58	0.67	
Observations	49	49	

**Fig. 2.** Average time spent on monitoring by behavioral types. Behavioral types are as follows: 0, free rider; 1, other types; 2, weak conditional cooperator; 3, conditional cooperator. Mean  $\pm$  SEM per type.



mine payoffs (38). Because players in the second decision could make their contribution contingent on the contribution of the other player, the experiment allowed for a clean identification of conditional cooperation as well as other types of behavior. A player is a conditional cooperator if his contribution increases with the contribution of the other player, a player who contributes zero independent of what the other player contributes is a free rider.

The exact criteria used to identify behavioral types together with their relative shares in our total sample are listed in Table 1. Thirty-four percent of the participants behaved as conditional cooperators and contributed more to the public good the more the other player contributed, such that the average correlation between self and partner player is high and highly significant [mean Spearman's rank correlation ( $\rho$ ) = 0.99,  $P \le 0.001$ ]. Another 12% behaved as so-called weak conditional cooperators (mean Spearman's  $\rho = 0.86, P < 0.05$ ). Free riders formed the second important type of behavior (11%); they either contributed zero to the public good regardless of the other player's contribution or at most one Birr in one of the seven possible decisions and zero in the remaining six decisions. The observed shares in our data fall within the range documented by previous laboratory experiments with student participants (10–13).

The distribution of the main behavioral types within and across the different forest user groups is illustrated in Fig. 1. Groups vary in their share of behavioral types, particularly in the share of conditional cooperators and free riders. In groups with more conditional cooperators, free rider shares are smaller (Spearman's  $\rho = -0.45$ , P = 0.001), suggesting that behavioral norms differ across groups. A plausible explanation may come from cultural transmission dynamics, which are able to generate within-group uniformity and between-group differences in behavioral norms (41, 42) (SOM text).

Forest user groups with larger shares of conditional cooperators exhibit better outcomes on average, whereas groups with larger free rider shares exhibit on average worse outcomes (Fig. 1). We estimated the impact of conditional cooperation on forest management outcome by means of a linear regression of the forest management outcome (PCT) on the share of conditional cooperators in the respective group, controlling for relevant structural factors such as elevation, group size, female shares, heterogeneity in livestock ownership, market distance, and time (Table 2). Our assumption regarding the direction of causality has its basis in established theoretical works (7) and laboratory experimental evidence (11, 15, 16). Results from further statistical analyses of our data,

including instrumental variables regression, corroborate this assumption (SOM text).

Model 1 (Table 2) considers the effect of structural variables in the linear regression alone, showing that the farther a group is located from the market, the lower is its forest management outcome (P = 0.000). Responses in the household as well as community surveys revealed that better market access allows members to earn cash income by selling forest products. As a result, groups that are closer to the market take stronger interest in forest management activities. Further, the time dummy has a strongly positive effect on the forest management outcome (P = 0.000), indicating that groups established earlier have better outcomes. We postulate that this effect is due to the time it takes young trees to grow to affect forest outcomes (SOM text). None of the other control variables in the regression have a robust significant effect on forest management outcome (SOM text).

Model 2 shows the effect of conditional cooperation on forest management outcome controlling for the structural variables. A larger share of conditional cooperators in a forest user group has a significantly positive effect on the forest management outcome (P = 0.000). Ceteris paribus, a 10% increase in the share of conditional cooperators increases forest management outcome on average by five PCT per hectare. In terms of elasticity at the mean, a 1% increase in the share of conditional cooperators increases the number of trees by 0.27%. In comparison, an increase in market distance by 1 hour of walking time reduces the forest management outcome on average by 21 PCT per hectare. In terms of elasticity at the mean, a 1% increase in the market distance decreases PCT by 0.73%. Further, groups that were established about 3 years earlier have on average 32 more PCT per hectare, ceteris paribus. Our results are robust even when we considered weak and strong conditional cooperators jointly (table S17), used weighted least squares regression to account for differences in sample size (table S13), used different proxies to measure socioeconomic structural factors (table S14 and S15), or controlled for demographic variables, such as age, education, and family size (table S16). We also interacted conditional cooperators with market distance and time but found no interaction effects on the outcome. Overall, conditional cooperators account for 9% of the variation in the forest management outcome. We got analogous results when we categorized groups by their share of free riders. As expected, larger free rider shares have a significantly negative effect on the forest management outcome (P = 0.000). Ceteris paribus, a 10% increase in the share of free riders leads to an average drop in forest management outcome by almost seven PCT per hectare (table S18).

In part, the positive correlation between the share of conditional cooperators and forest management outcome is likely to be due to conditional cooperators contributing more to the conservation of the forest. For example, in the unconditional decision in our experiment, conditional cooperators contributed 40% of their endowment to the

**Table 3.** Costly monitoring, conditional cooperation, and structural variables. The dependent variable is the average time a group member spends monitoring the forest, measured in hours per month. The independent variables are the share of conditional cooperators in a group, market distance, and time. Additional controls include monitoring difficulty, group size, share of female members, and heterogeneity in livestock ownership. OLS estimates with robust standard errors in parentheses. \*\*\*P < 0.01, \*\*P < 0.05.

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Variables	1	2	
Conditional cooperator share		23.782*** (8.700)	
Market distance	-5.972*** (1.518)	-4.951*** (1.543)	
Time	11.428*** (3.814)	9.079** (3.477)	
Constant	49.467*** (16.464)	42.092** (15.553)	
Additional controls	Yes	Yes	
Adjusted r <sup>2</sup>	0.31	0.42	
Observations	45	45	

public good compared with 15% by free riders [Kruskal-Wallis test,  $\chi^2$  (3) = 67.40, P = 0.000]. However, theory and empirical evidence suggest that conditional cooperators will not be able to sustain cooperation alone in the presence of less cooperative types unless enforcement mechanisms, such as costly monitoring and punishment, are available and used. Our experimental data confirm this. Conditional cooperators contributed significantly less to the public good if they believed that the other player contributed less (Spearman's  $\rho$  = 0.36, P = 0.000) or if there were more free riders in their group (Spearman's  $\rho$  = -0.46, P = 0.001).

Thus, forest management can only be successful if groups with larger shares of conditional cooperators also invest more in the enforcement of cooperation, a prediction that is confirmed by our data. In the field setting, forest patrols conducted by group members were the main enforcement activity allowing for the detection and punishment of free riders. Models of cultural evolution (18) and experimental evidence (17, 24, 25) suggest that conditional cooperators are more likely to monitor in relation to other behavioral types. We tested this by using survey data on monitoring behavior collected independently at both an individual and a community level. At the individual level, we found that, among the behavioral types, conditional cooperators indeed monitor the most, spending on average 32 hours per month on monitoring (Fig. 2); this is 1.5 times more than what free riders invested in monitoring [Kruskal-Wallis test,  $\chi^2$  (3) = 25.04, P = 0.000]. The result is corroborated by a regression analysis on the group level (Table 3) showing that groups with larger share of conditional cooperators invest on average more time monitoring their forest (P = 0.010). Ceteris paribus, a 10% increase in the share of conditional cooperators increases the time spent on monitoring by 2.5 hours on average. In terms of elasticity at the mean, a 1% increase in the share of conditional cooperators increases time spent monitoring by 0.28%. A similar result is obtained when we measure monitoring behavior by aggregating individual responses in the household questionnaire at the group level (table S20). Analogously, a larger share of free riders in a group has a significantly negative effect on monitoring (tables

S19 and S20). In sum, better forest management outcomes are not only a result of conditional cooperators being more likely to abide by the local rules of the group but also being more willing to enforce these rules at a personal cost.

Our findings establish that, in addition to structural factors, behavioral motives such as the norm of conditional cooperation are an important element behind forest users' achievement in managing their commons. The results identify key complementarities between experimental measures of conditional cooperation, field outcomes on commons management, and survey measures on costly monitoring. Together, these results not only provide external validity to laboratory experiments (30) but also advance the frontiers of previous work on commons management. Our findings entail a number of implications for realworld common property regimes. In line with previous research, the data show that voluntary cooperation in commons management is not a pipe dream but an empirical fact. However, voluntary cooperation is fragile because the individual willingness to cooperate depends on the cooperation of others. This gives rise to important social interaction effects and implies that expectations individuals hold about the cooperation of others play a critical role. Conditional cooperators who see (or expect) others defect will exhibit very different behavior than conditional cooperators who see (or expect) others cooperate. Common property management can take this into account by designing institutions that provide incentives for purely self-regarding individuals to cooperate and at the same time foster the norm of conditional cooperation (43). Punishment institutions that sanction free riding and coordinate expectations on cooperation are one possible solution. In these institutions, local enforcement may play an important part (20, 21), but this depends on the behavioral type composition of a group. As our data confirm, conditional cooperators play a key role in this regard: Not only do they contribute more to the firstorder public good, but they are also more willing to contribute to the second-order public good, that is, to enforce first-order cooperation.

Overall, our study contributes to the accumulating evidence suggesting that an effective solution to commons problems is not based on panaceas (44) and incentives for self-regarding individuals alone but explicitly takes into account the complex interplay of behavioral norms and, more generally, the "ecology" of different interacting types (11, 16). Policies aimed at conserving the commons may integrate the results of behavioral economic research and not only focus on the importance of structural factors but also consider the intrinsic and heterogeneous motivations of users of the commons to cooperate voluntarily.

Lastly, our results are also important for the evolution of group beneficial behaviors. The findings that groups vary in their share of conditional cooperators as well as other behavioral types and that there is a positive covariation between conditional cooperation and costly monitoring at both individual and group levels are in line with models of gene-cultural coevolution (18, 45). These models predict that, in groups where costly enforcement is prevalent, cooperation is expected to be higher; this costly enforcement together with cultural transmission mechanisms is expected to lead to the emergence of stable between-group differences on which cultural group selection might then operate, ultimately paving the way for the spread of group beneficial behaviors in the population.

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### Supporting Online Material

References and Notes

www.sciencemag.org/cgi/content/full/330/6006/961/DC1 Materials and Methods SOM Text Fig. S1 Tables S1 to S20

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# The Role of Discharge Variation in Scaling of Drainage Area and Food Chain Length in Rivers

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Food chain length (FCL) is a fundamental component of food web structure. Studies in a variety of ecosystems suggest that FCL is determined by energy supply, environmental stability, and/or ecosystem size, but the nature of the relationship between environmental stability and FCL, and the mechanism linking ecosystem size to FCL, remain unclear. Here we show that FCL increases with drainage area and decreases with hydrologic variability and intermittency across 36 North American rivers. Our analysis further suggests that hydrologic variability is the mechanism underlying the correlation between ecosystem size and FCL in rivers. Ecosystem size lengthens river food chains by integrating and attenuating discharge variation through stream networks, thereby enhancing environmental stability in larger river systems.

ood chain length (FCL) is a key measure of  $\triangleleft$  the vertical structure of food webs (1, 2) that determines energy flow through ecosystems (3), carbon exchange between freshwater ecosystems and the atmosphere (4), and nutrient cycling (5). FCL is also important to human health, influencing the bioaccumulation of contaminants in top predators consumed by humans (6). Ecological theory suggests that FCL should increase with energy supply (7, 8), the available energy pool (9), and environmental stability (8). In contrast, empirical studies have revealed weak effects of energy supply (10-12) and contradictory reports of negative, positive, or null effects of environmental variation on FCL (10, 12). Recent studies show a strong effect of ecosystem size on FCL in lakes and on oceanic islands (11, 13), but the mechanisms underlying this relationship remain unclear (12, 14).

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In river ecosystems, climate change and human appropriation of fresh water are altering discharge variability and the frequency of intermittency across the globe (15). These hydrologic alterations have implications for the structure of river food webs. FCL in rivers may vary with the stability of the environment [for example., age area), and energy supply. All three are correlated because the magnitude of high flows, channel geometry, and the relative supply of aquatic and terrestrial energy sources (such as algae and leaf litter from riparian trees, respectively) vary with drainage area (16-18). Thus, flow variation and other putative controls of FCL may scale with drainage area and mechanistically link ecosystem size to FCL. To date, no single study has addressed the simultaneous effects of energy supply, environmental variation, and ecosystem size-and correlations among these drivers-on the length of food chains in rivers or any other ecosystem.

We tested the role of ecosystem size, environmental stability, and energy supply on FCL in 36 rivers in North America. We define FCL as the maximum trophic position of stream-dwelling consumers measured via a stable isotope approach, which can accommodate omnivory and non-integer values of FCL (19). Our analysis expands on previous work on FCL in three ways. First, our study sites include a comprehensive

range of values for all putative controls of FCL (20): a variation of >6 orders of magnitude in ecosystem size [drainage area  $(A_d) = 0.35$  to  $10^6$  km<sup>2</sup>], a variation of >3 orders of magnitude in energy supply [gross primary production (GPP) = 0.06to 18.9 g of O<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>], and high-flow variation  $[\sigma_{HF}(21) = 0.03 \text{ to } 12.9]$ . Our study sites also include both perennial and intermittent rivers, providing us with an opportunity to quantify how river drying affects riverine food web structure. Second, we used a hybrid of spectral and extreme event statistics to quantify environmental variation [( c 1/(environmental stability)], which provides a quantitative measure of discharge variation with reference to long-term discharge patterns (21). Third, we used path analysis to quantify and compare the path coefficients of drainage area - FCL and drainage area→flow variation→FCL relationships. In doing this, we asked whether ecosystem size has direct effects on FCL, or whether these effects are indirect and mediated via scaling between drainage area and flow variability (22).

We found that FCL increased with ecosystem size and decreased with  $\sigma_{HF}$  but was unrelated to energy supply (Fig. 1), which is consistent with previous findings (23–25). Ecosystem size had similar effects on FCL when measured as drainage area or cross-sectional area (fig. S1). Food chain length ranged from  $\sim$ 3 (predator) to nearly 5 (tertiary predator), matching the largest range of variation in FCL of any ecosystem (10, 11). Top predators in 32 streams were fish, and these taxa were sufficiently large to be piscivorous in 29 sites (table S1). In intermittent streams, the top predator was consistently an invertebrate or an insectivorous fish.

Our results suggest that the strong effect of ecosystem size on FCL arises in part from a relationship between drainage area and flow variation and strong control of FCL by high- and low-flow events.  $\sigma_{HF}$  scaled with drainage area (Fig. 2A), but the power of the scaling relationship was significantly less steep and the mean  $\sigma_{HF}$  value was significantly higher in intermittent than in perennial rivers. Significant negative powers in both cases indicate that flow variation declines with drainage area. Attenuation of discharge variation results from spatial averaging in larger basins of asynchronous precipitation and high flows occurring in upstream portions of the drainage network. FCL increased