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ORIGINAL ARTICLE

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Effects of a predatory fish on a tropical detritus-based food web

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Abstract In contrast to that for grazing systems, relatively little information exists for trophic cascades in detritus-based stream food webs, which are predominant in forested headwater streams. Predator–prey interactions are thought to be weak in these systems, but studies are very scarce, their results are equivocal, and they do not separate the effect of direct consumption from a behavioural response of shredders. We examined the effect of predatory fish on leaf litter breakdown in headwater tropical Australian streams at three levels: (1) the behavioural response of shredder species to predator presence as indicated by chemical cues; (2) the rates of leaf breakdown resulting from shredder activity; and (3) the relationship between shredder species richness and leaf breakdown rates. Our results suggest that predatory fish can have a trait-mediated effect on detritus-based food webs in streams, by reducing consumer activity. We identified reductions in short-term overall activity in response to the presence of predatory fish cues, comparable to those found for grazers. We also observed a visible, albeit statistically non-significant, reduction in consumption rates. Shredder species richness did not affect leaf breakdown rates, and fish presence did not modify this relationship or the differences in breakdown rates among species, suggesting that the overall reduction in leaf breakdown caused by fish presence is due to a reduction in activity in every species. Thus, our laboratory studies have shown that there can be a behavioural basis for trait-mediated trophic cascades linked to fish presence in detrital food webs in streams. However, the strength of fish effects depends on environmental circumstances, and field studies of litter breakdown in streams with and without predatory fish are required if we are to elucidate the ecological significance of our observations.

Keywords Behaviour · Chemical cues · Leaf breakdown · Trophic cascade · Tropical streams

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Introduction

Populations of stream macro-invertebrates may exist in habitat patches with and without predatory fish (Caudill and Peckarsky 2003). Populations of prey living in habitats where predatory fish are present are often able to detect them through water-borne chemical cues and respond with behavioural changes that lower predation risk (Chivers 1998). This phenomenon and its consequences at the population, community and ecosystem levels have been extensively studied for grazers, mainly mayflies (Flecker and Townsend 1994; Scrimgeour et al. 1994; McIntosh and Townsend 1995; Huryn 1998; McIntosh and Peckarsky 2004), but studies that simultaneously address more than one ecological level are comparatively rare (Townsend 2003). Typically, grazers respond to predatory fish cues by decreasing their overall activity level, including foraging (Scrimgeour et al. 1994; Huhta et al. 1999; Miyasaka and Nakano 2001). Reduced foraging activity results in lower grazing rates, which, in turn, may lead to increases in the abundance of the periphytic algae that grazing macro-invertebrates consume, thus generating a trophic cascade (Flecker and Townsend 1994; Huryn 1998) that may be fully trait-mediated (i.e., not dependent on numerical changes of the organisms involved—McIntosh and Townsend 1996; Schmitz et al. 1997).

In contrast to that for grazing systems, relatively little information exists for trophic cascades in detritus-based food webs in streams (Oberndorfer et al. 1984; Konishi et al. 2001), particularly those based on the leaf litter entering the stream from the surrounding terrestrial systems. It has been proposed that weak interactions, which would not be conducive to the cascading effects inherent in traditional grazing models, may be common in detrital food webs (Johnson and Wallace 2005). However, the effects of predators on leaf litter breakdown rates have been little explored and are equivocal. While Oberndorfer et al. (1984) and Konishi et al. (2001) found a reduction of leaf breakdown when predators (invertebrates and fish, respectively) were present, Reice (1991) found no effect of predators (fish) on leaf breakdown rates, and Ruetz et al. (2002) found that predators (fish) can affect leaf breakdown but that the direction of the effect was dependent on which shredder taxa were present. Moreover, those studies that have shown a negative effect of predators on leaf breakdown rates have not separated the effect of direct consumption from a behaviourally mediated response of shredders. Studies on shredders' behavioural responses to fish chemical cues are very scarce (Short and Holomuzki 1992; Åbjörnsson et al. 2000; Greig and McIntosh 2006).

Headwater streams in the Australian wet tropics are detritus-based systems that harbour a diverse and numerically important shredder guild (Cheshire et al. 2005), providing an opportunity for the study of behavioural and trophic interactions in detritus-based stream food webs. The same shredder species inhabit both the upper and lower parts of these streams, while the abundance and diversity of potential predatory fish decreases as one moves upstream, with fish generally absent in the uppermost reaches. Hence, potential predation intensity varies spatially and may be lacking in some patches of habitat, but the scenario is still conducive to the evolution of anti-predator responses (Tikkanen et al. 1996).

The objective of our study was to examine the potential influence of the presence of predatory fish on leaf litter breakdown rates in headwater tropical Australian streams. We explored the effects of fish at three levels: (1) the behavioural response of shredder species to predator presence, as indicated by chemical cues; (2) the rates of leaf breakdown resulting from shredder activity; and (3) the relationship between shredder species richness and leaf breakdown rates.

The last level of our exploration is directly linked to an area of intense, current, scientific debate: it examined the relationship between biodiversity and ecosystem function, an issue of critical importance in the face of increasing diversity loss resulting from anthropogenic causes. There exists some consensus about the effect of plant diversity on primary productivity (Loreau et al. 2001), but evidence of the effects of consumer diversity on breakdown rates is controversial (Jonsson and Malmqvist 2000, 2003; Boyero et al. 2007). Cardinale et al. (2000) showed that the environmental context (e.g. spatial heterogeneity, disturbance frequency, temperature) can affect the relationship between diversity and ecosystem processes, and we hypothesize that predator presence can also influence this relationship.

Methods

Shredder and predator species

The four studied shredder species were *Anisocentropus kirramus* Neboiss (Trichoptera: Calamoceratidae), *Lectrides varians* Mosely and *Triplectides gonetalus* Morse and Neboiss (Trichoptera: Leptoceridae), and *Atalophlebia* sp. (Ephemeroptera: Leptophlebiidae). These species are the most abundant of a more diverse shredder guild in streams in the Australian wet tropics (Cheshire et al. 2005). Shredders for all experiments were collected from the upper [~800 m above sea level (a.s.l.)], fishless reaches of Birthday Creek (18°59′ S, 146°10′ E) and Camp Creek (also called Little Birthday Creek, a tributary of Birthday Creek—18°58′ S, 146°10′ E) in the late dry season (September to November, 2004). Birthday and Camp Creeks are upland rainforest streams located in the Burdekin River catchment, within the Paluma Range National Park, North-eastern Queensland, Australia.

We used as predatory fish the eastern rainbowfish, *Melanotaenia splendida* (Peters), which is widely distributed within its range and inhabits many lotic and lentic habitats, including Birthday Creek downstream of the invertebrate collection sites. *M. splendida* is a generalist predator with a broad diet that includes a variety of stream macro-invertebrates (Pusey et al. 2000; Allen et al. 2002). Those traits, and good acclimation to confinement, made it an appropriate choice for our experiments. Rainbowfish were collected from the lower reaches of streams in the area and kept in a 300 l aquarium at 26°C (fish density in the aquarium 0.05 individuals per litre). They were fed daily with commercial food for aquarium fishes ad libitum.

Experiment I: effects of rainbowfish cues on shredder individual behaviour

To assess the extent to which the four shredder species altered their behaviour when exposed to chemical cues from a predatory fish, we conducted the following laboratory experiment. Immediately after collection, macro-invertebrate shredders were taken to the laboratory and kept in plastic containers filled with commercial bottled water. Food was provided as leaves of *Apodytes brachystylis* Mueller (Icacinaceae), a common riparian tree species along Birthday and Camp Creeks, which shredders consume readily (Pearson and Connolly 2000). Temperature was maintained at 20°C, and a 12:12 h light:dark photoperiod was simulated to mimic natural conditions. Containers were not aerated, as the animals were collected from amongst leaf litter in still or slow-flowing water and their numbers were kept low relative to water volume in each container.

For each experimental trial, an individual was placed in a plastic container (25 cm × 11 cm) filled with 200 ml of mineral water and was left for 25–30 min to acclimate. Pilot observations had indicated that this would be ample time for individuals of all species to resume apparently normal behaviour. The experiment consisted of two phases, each lasting 3 min. Between the first and the second phases, we added 6 ml of water to the container using a plastic syringe and a length of plastic tubing. Water addition was as careful and gentle as possible to minimize disturbance. In control runs, we added mineral water, whereas, in treatment runs, we added water from the aquarium, which, hence, contained chemical cues from rainbowfish. The containers were thoroughly washed with mineral water between trials, and trials were repeated until we had tested 30 individuals of *A. kirramus* and *L. varians* (15 control and 15 treatment) and 20 individuals of *T. gonetalus* and *Atalophlebia* sp. (10 control and 10 treatment). These differences were due to different availability of each species at the time of collection. Each individual was tested once only.

In each phase of a trial, we recorded the time (seconds) that the animal was active (walking, swimming, or moving the legs), using a stopwatch. Then we computed the difference between time active in phase 1 and time active in phase 2 as a measure of the effect of the chemical stimulus. The difference in activity between phases was then analysed with a full-factorial, two-way analysis of variance (ANOVA), with treatment (control or fish odour) and shredder species as main factors.

Experiment II: effects of rainbowfish chemical cues on leaf breakdown rates and their relationship with shredder species richness and identity

We explored the influence of fish chemical cues on leaf breakdown rates by shredders, and on the relationship between shredder species richness and leaf breakdown rates, with a mesocosm experiment. We expected leaf breakdown to be reduced, when fish chemical cues were present, by a reduction in shredder activity. Intraspecific interference is high in the studied shredders (Boyero and Pearson 2006), and increasing the number of species while decreasing the number of individuals per species increases leaf breakdown rates in laboratory experiments (Boyero et al. 2007). Under this scenario, we expected fish effects to be less marked the higher the number of shredder species present, due to differences in activity reduction among shredder species.

Experimental mesocosms were set up in 65 l plastic tanks (52 cm × 33 cm × 38 cm) filled with dechlorinated tap water and aerated with aquarium pumps. On the bottom of each tank we placed eight transparent plastic cages (15 cm × 10 cm × 5 cm). The lid of each cage had a mesh screen window, and the sides and bottom of the cages were perforated so that water could circulate but experimental animals (fish and macro-invertebrates) could not. Each cage was supplied with one pre-weighed air-dried *A. brachystylis* leaf and was randomly assigned one of the following combinations of shredders: (1) control (no shredders); (2) *Anisocentropus* (six individuals); (3) *Lectrides* (six individuals); (4) *Triplectides* (six individuals); (5) *Anisocentropus* and *Lectrides* (three individuals each); (6) *Anisocentropus* and *Triplectides* (three individuals each); (7) *Lectrides* and *Triplectides* (three individuals each); and (8) *Anisocentropus*, *Lectrides* and *Triplectides* (two individuals each). *Atalophlebia* was not used in this experiment because of the low availability of individuals at the time of collection. The control cage without shredders was used to measure microbial leaf breakdown and leaching in each mesocosm.

Each of the tanks holding the cages was supplied with either one rainbowfish (fish effects treatment) or no fish (controls). The macro-invertebrates in cages within tanks containing a fish could receive chemical, visual and mechanical cues from it but were not subject to direct predation. We performed two runs of the experiment, each one lasting 2 weeks, after which time leaves and shredders were collected, taken to the laboratory, dried at 50°C for 48 h and weighed to the nearest milligramme. There were some instances of fish mortality, and data from those containers were discarded. The total number of replicates was six for the fish treatment and seven for controls.

Leaf mass loss (LML—corrected by the subtraction of leaf mass loss in control cages) and LML divided by shredder biomass (in milligrammes) were analysed with a doubly nested (split-plot), multi-way, analysis of covariance (ANCOVA). Container identity was a block factor (plot). Experimental run (first and second) and fish treatment (control and fish effects) were between-blocks (main plot) factors. Accordingly, the mean sum of squares (SS) associated with container was used as error term to test the significance of the "between-blocks" terms in the ANCOVA model. As some containers were discarded from analyses due to fish mortality, container was doubly nested within both run and fish treatment. The particular combination of shredder species ("shredder identity") and shredder species richness (one to three species, nested within shredder identity) were "within-blocks" (sub-plot) factors, and shredder survival (percentage) was a covariate. It was necessary to include shredder identity as a factor, as there were three levels of 1-species richness, three levels of 2-species richness, and one level of 3-species richness. LML and LML per shredder milligramme were log-transformed, and survival was transformed to the arcsine of the square root, to meet the assumptions of parametric analysis (Zar 1999). We tested for homogeneity of slopes of the LML–survival relationship across combinations of fish treatment, run and species richness for both LML and LML per shredder milligramme. In both cases slopes were clearly not significantly different among groups ($F_{11,54}$ = 0.59, P = 0.83 and $F_{11,54}$ = 0.47, P = 0.91, respectively) and, consequently, we subsequently used a common-slope model in further analyses.

Results

Experiment I: effects of rainbowfish cues on shredder individual behaviour

The addition of fish chemical cues elicited a general, significant, reduction in the activity of shredders, but the extent of the reduction was different among species (Table 1, Fig. 1), being significantly greater in *L. varians* than in the other three species, which showed no difference among them (post-hoc Tukey tests). As the interaction between treatment and species was significant (Table 1), we performed separate ANOVAs to explore the response of different species. *A. kirramus* and *L. varians* showed a significant response to fish chemical cues ($F_{1,28} = 11.64$, $P = 0.0020$, and $F_{1,28} = 66.31$, $P < 0.0001$, respectively), while the response of *Atalophlebia* sp. and *T. gonetalus* was marginally significant at the 0.05 level ($F_{1,18} = 3.97$, $P = 0.0617$, and $F_{1,18} = 3.08$, $P = 0.0963$, respectively).

Experiment II: effects of rainbowfish chemical cues on leaf breakdown rates and their relationship with shredder species richness and identity

LML and LML per shredder milligramme were higher in the second experimental run than in the first, and they tended to be higher in the absence of fish, although this difference was not statistically significant (Table 2, Fig. 2). LML increased with survival (Table 2). LML per shredder milligramme varied with shredder identity (Table 2), being higher in treatments with only *L. varians* than in all other treatments (post-hoc Tukey tests, $P < 0.00014$ in all cases). Average survival rate was 53% for shredders and 60% for fish.

Table 1 Results of ANOVA showing differences in shredders' behavioural responses (reduction in activity after the addition of waterborne chemical cues) with treatment (control/fish odour) and species (*A. kirramus*/*L. varians*/*T. gonetalus*/*Atalophlebia* sp.) in experiment I. Degrees of freedom (*df*), sum of squares, *F* statistic and probabilities are shown

Parameter	*df*	SS	*F*	*P*
Fish treatment	1	14,731.21	48.37	< 0.0001
Species	3	8,515.26	9.32	< 0.0001
Fish treatment × species	3	6,057.75	6.63	0.0004
Error	92	28,017.23		

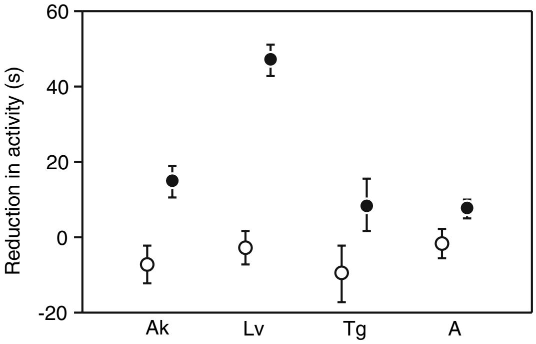

Fig. 1 Reduction in activity (in seconds) after the addition of water with (treatment, *closed circles*) or without (control, *open circles*) fish chemical cues in experiment I. *Ak Anisocentropus kirramus*; *Lv Lectrides varians*; *Tg Triplectides gonetalus*; *A Atalophlebia* sp. *Bars* represent standard errors

Discussion

Our results suggest that predatory fish can have trait-mediated effects on detritus-based food webs in streams. In our experiments we identified reductions in short-term overall activity of shredders in response to the presence of predatory fish cues in laboratory conditions. We also observed a visible, albeit statistically non-significant, reduction in consumption rates. Previous studies that have detected fish effects on stream food webs based on leaf litter apparently highlighted direct effects, with fish affecting leaf breakdown through a reduction in the abundance of macro-invertebrate shredders (Konishi et al. 2001; Ruetz et al. 2002; Greig and McIntosh 2006). Comparable reductions in activity and, as a consequence, resource processing rates, have been shown to result in community-level and ecosystem-level effects of fish presence in food webs based on epilithic algae (McIntosh and Townsend 1996). Hence, our findings suggest that similar mechanisms may also be relevant for detrital food webs, which are central to the ecology of many tropical and temperate stream ecosystems (Cheshire et al. 2005). They also indicate that fish introductions into previously fishless areas—a widespread and growing form of human impact—may have far-reaching effects on stream food webs, beyond those currently reported (Townsend 2003).

Experiment I showed that the four shredder species tested reduced their movements when exposed to chemical cues from rainbowfish. As far as we know, such a decrease in activity when exposed to predatory fish odour has not been previously reported for caddisfly shredders, though reductions in activity are a very general anti-predator response (Werner and Anholt 1993). In the specific case of predatory fish, activity reductions have been reported for a variety of stream macro-invertebrates (Kohler and McPeek 1989) including crustacean shredders (Holomuzki and Hoyle 1990; Short and Holomuzki 1992; Åbjörnsson et al. 2000) and cased, grazer, caddisflies of the genera *Agapetus* (Malmqvist 1992) and *Glossosoma* (Kuhara et al. 2001). However, Kohler and McPeek (1989) failed to detect any response by another species of *Glossosoma*, and Malmqvist (1992) similarly found no clear response of *Silo pallipes* to fish chemical cues. Our own results also highlighted interspecific differences in the reaction to predator cues, but they were of a smaller magnitude, as all four species decreased their movement rates to some extent. This decrease was, however, significantly greater in the two

Table 2 Results of ANCOVAs showing the effect of fish treatment (control/fish odour), experimental run, container, shredder species richness (1/2/3 spp.) and identity, and shredder survival, on leaf breakdown in experiment II. Degrees of freedom (*df*), sum of squares, *F* statistic and probabilities are shown. Error terms are indicated within *parentheses* when different from the general error term. Significant results are in *bold type*

Parameter	*df*	SS	*F*	*P*
LML				
Fish treatment	1	2,054.51	1.72	0.2223
Run	1	19,168.88	16.03	**0.0031**
Fish treatment × run	1	223.55	0.31	0.5808
Container (fish treatment × run) (main plot error)	9	10,760.03		
Spp. richness (spp. identity)	4	4,001.06	1.37	0.2511
Spp. richness	2	584.62	0.40	0.6701
Run × spp. richness	2	784.33	0.54	0.5851
Fish treatment × spp. richness	2	414.90	0.28	0.7523
Run × fish treatment × spp. richness	2	1,003.75	0.69	0.5044
Survival	1	5,007.70	6.90	**0.0107**
Error	65	46,166.95		
LML/shredder biomass				
Fish treatment	1	38.39	3.03	0.1155
Run	1	254.99	20.15	**0.0015**
Fish treatment × run	1	0.41	0.03	0.8607
Container (fish treatment × run) (main plot error)	9	113.89		
Spp. richness (spp. identity)	4	1,089.52	18.28	**< 0.0001**
Spp. richness	2	47.44	1.59	0.2112
Run × Ssp. richness	2	15.83	0.53	0.5903
Fish treatment × spp. richness	2	15.79	0.53	0.5911
Run × fish treatment × spp. richness	2	29.74	1.00	0.3741
Survival	1	28.79	1.93	0.1692
Error	65			

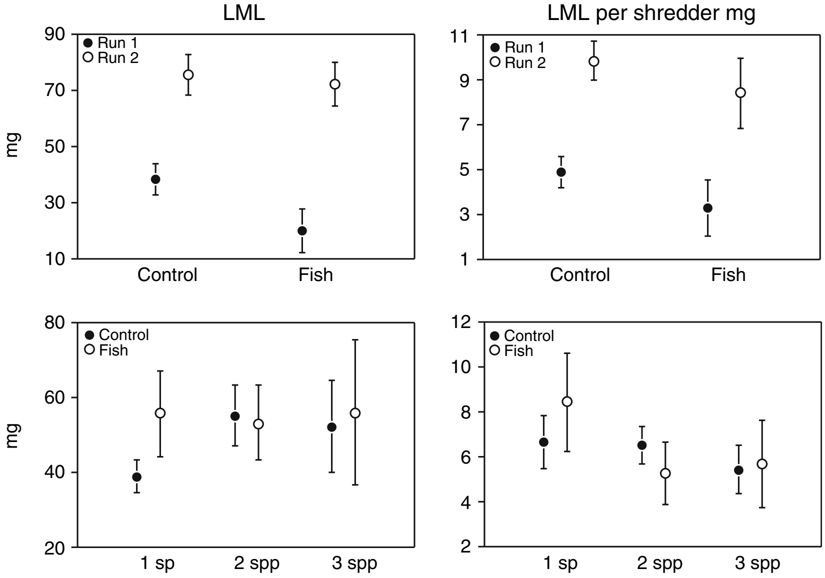

Fig. 2 Variation of LML (*left*) and LML per shredder milligramme (*right*) with treatment (control/fish odour) and experimental run (*above*); and treatment and shredder species richness (1/2/3 species) (*below*), in experiment II. *Bars* represent standard errors

most abundant species, *A. kirramus* and *L. varians*, which are also the faster leaf processors and account for most leaf breakdown in these streams (Boyero et al. 2006). High impact of fish presence upon the most active shredder species should make behavioural shifts such as those identified in experiment I more likely to translate into lower overall leaf litter breakdown rates and, hence, have consequences at higher ecological levels.

The findings of experiment II seemed consistent with those of experiment I. We observed a reduction in leaf consumption rates as a sublethal effect of fish presence. Although apparent and of a comparable magnitude in both experimental runs, this decrease, however, was not statistically significant, possibly due to the reduced statistical power of the test that resulted from the exclusion from the analyses of containers where fish had died. As the experimental design prevented the fish from reducing the numbers of shredders, the lowered leaf breakdown must have occurred through changes in consumer behaviour such as those indicated by experiment I. Our results suggest that the indirect effects of predatory fish on leaf litter breakdown may extend to caddisfly shredders, often a major component of the shredder guild (e.g. Dangles 2002; Cheshire et al. 2005), and to situations where more than a single shredder species is present. Similar concurrent decreases in activity and leaf breakdown rates had been previously reported for two crustacean shredder species exposed to fish odour—*Lirceus* *fontinalis* (Short and Holomuzki 1992) and *Gammarus pulex* (Åbjörnsson et al. 2000).

The results from experiment II also suggest that the effects of predatory fish on leaf breakdown rates can be context-dependent. The impact of fish presence on overall leaf breakdown was lower in the second run of the experiment, when breakdown rates were significantly higher in both mesocosms with and without fish. Temperature was higher in the second run and, hence, shredder metabolic rates (and therefore processing rates) must have been somewhat higher (Rostgaard and Jacobsen 2005). However, temperature differences were small (averages of 20.3°C and 21.8°C) and, accordingly, metabolic increases must have been modest (Q_{10} values for macro-invertebrates usually range from 1 to 3; Rostgaard and Jacobsen 2005) and cannot account for the high differences in leaf breakdown between experimental runs. Some other factor must have been at work, but we currently feel unable to speculate on its identity.

Shredder species richness did not influence leaf breakdown rates in experiment II, but the identity of shredder species affected breakdown rates when corrected per shredder biomass, with higher rates for *L. varians*, as shown in other studies (Bastian et al. 2008; Boyero et al. 2007). However, the presence of fish had no effect on differences in breakdown rates among species, suggesting that the overall reduction in leaf breakdown caused by fish presence is due to a reduction in activity in every species (as suggested also by experiment I).

In summary, our results showed that the behavioural basis for trait-mediated trophic cascades linked to predatory fish presence/absence in food webs based on leaf litter exists in some of the most functionally important shredders (Cheshire et al. 2005) in streams of the Australian wet tropics (experiment I) and that such behavioural mechanisms may result in lowered rates of leaf breakdown in laboratory conditions (experiment II). However, our findings also indicated that the extrapolation of those findings to field conditions requires caution, as the strength of indirect fish effects was not high and appeared to be substantially influenced by environmental circumstances. Moreover, mechanisms that may lessen the impact of fish presence, which do not operate in the controlled laboratory settings, may come into play in the more complex situation of natural systems (Greig and McIntosh 2006). Additional field studies of litter breakdown in streams with and without predatory fish would clearly be useful in further elucidating the ecological significance of our observations.

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