Flood disturbance mediates the strength of stream trophic cascades caused by trout

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Abstract

Trophic cascades are important features of aquatic ecosystems, but much variation in their strength remains unexplained. Disturbance could restrict cascade occurrence by limiting predator distribution, and increase cascade strength by lowering defended herbivore abundance. These possibilities were investigated in 20 New Zealand rivers varying both in flooding disturbance (measured by bed movement) and presence of non-native predatory trout. Trout were often, but not always, associated with indirectly increasing algal abundance compared to similar rivers with native galaxiid fishes. Floods explained variation in cascades by (1) resetting algal abundance such that algal minima were related to bed movement; (2) preventing occurrence by restricting trout abundance in the most disturbed rivers; and (3) increasing potential cascade strength by removing defended herbivores. These observations indicate strong nonlinear influences of disturbance on both trophic cascade occurrence and maximum strength which will be important to consider as climate change alters disturbance regimes.

Trophic cascades have important influences on ecological communities (Estes et al. 2011), but their occurrence and strength is likely affected by many other influences (Rogers et al. 2020). Despite their importance, many of those variations in cascade strength still remain unexplained (Shurin et al. 2002, 2006; Borer et al. 2005; Su et al. 2021). Recent investigations suggest that examining spatial and temporal patterns in cascade strength will shed light on controls of cascade strength (Rogers et al. 2020).

Disturbance is likely an overlooked driver of variation in trophic cascade strength. Disturbance has typically been associated with reducing top-down influences because it can
decrease predator abundance (Menge and Sutherland 1987), but disturbance can also increase top-down effects (Thomson et al. 2002; Greig et al. 2013). For example, predator influence can increase when disturbance differentially removes herbivores with morphology that protects them from predation, leaving more vulnerable herbivores lacking such protections (Wootton et al. 1996; Power et al. 2008). These contingencies are associated with a trade-off between competitive ability and colonization (Tilman 1994), whereby species with morphological defenses are less vulnerable to predation but also less resilient following disturbance (Power et al. 2008). Thus, disturbance could both weaken cascade strength by limiting predators and increase it via effects on herbivores.

Flooding influences on river trophic cascades provide the opportunity to investigate such disturbance effects on cascade strength. A cascade in New Zealand rivers driven by non-native trout decreasing invertebrate grazing compared to native fishes is well-documented (Flecker and Townsend 1994), but is likely affected by disturbance since flooding is a prominent driver of New Zealand fish, invertebrate, and algal communities (Biggs et al. 1999; Jellyman and McIntosh 2020). In particular, the proportion of grazing invertebrates with cases or shells declines with flooding (Jellyman and McIntosh 2020). The top-down influence of trout also includes a large trait-mediated component whereby trout restrict the grazing behavior of herbivores (McIntosh and Townsend 1996), so disturbance-driven effects on abundance of vulnerable compared to defended herbivores should be influential (Nyström and McIntosh 2003). Non-native trout are more sensitive to flooding disturbance than native galaxiid fishes (McIntosh 2000; Boddy et al. 2020), so flooding should also influence trout most. This breadth of previous work provides a strong mechanistic platform for evaluating the drivers of cascade strength across a flooding gradient. Importantly, even though large numbers of predatory invertebrates are present, fish trophic omnivory means that these food webs function as three, rather than four, trophic level systems (Flecker and Townsend 1994).

To investigate drivers of cascade variability, I studied trout-induced trophic cascades in rivers spanning a large flooding gradient. I hypothesized that, by affecting herbivore and predator composition and abundance, flooding would alter cascade strength. I expected that disturbance effects on herbivore composition, driven by the trade-off between competitive ability and colonization, would initially strengthen top-down effects by removing predator-resistant herbivores. Weak positive effects of trout on algal abundance were anticipated in stable rivers where benign conditions meant most herbivores were protected with cases or shells. However, in intermediate disturbance rivers where disturbance likely reduces the abundance of protected herbivores, cascades should be strongest due to the vulnerability of remaining unprotected herbivores. Finally, I expected extreme flooding to prevent strong top-down interactions altogether by eliminating predatory trout and restricting algal growth.

**Materials and methods**

**Study sites**

Twenty rivers in the Waimakariri River catchment provided the largest possible range of flood-related bed disturbance while allowing comparison of fish effects (Table 1). Rainfall gradients combined with steep, eroding catchments produce disturbed braided rivers, lakes and springs produced stable beds, and existing information aided identification of sites lacking trout (due to barriers; McIntosh 2000). Rivers were associated with beech forest or grassland and were clear and largely unaffected by development; nutrient levels were low (soluble inorganic nitrogen $\leq 0.1$ mg L$^{-1}$ and soluble reactive phosphorus $\leq 0.03$ mg L$^{-1}$; Nyström et al. 2003); and pH was neutral (pH 6.5–7.8). Canopy cover, bed substrata, and widths varied but were unassociated with trout abundance (Table 1; McIntosh 2000).

**Disturbance measurements**

I measured flood-disturbance by following tracer particles incorporated into stream beds (following Townsend et al. 1997). Bed movement best reflects the stressors and disruptions to resources experienced by benthic communities, so reliably measures flood-related disturbance (Jellyman et al. 2013; Peckarsky et al. 2014). Painted cobbles, chosen to match the 50th, 75th, and 90th percentile classes of substratum, were placed into river beds (following Townsend et al. 1997), and their movement frequency assessed every ~ 50 d between March 1998 and February 2000. Multiple disturbance measures were possible (e.g., magnitude, frequency, time since), but highly correlated ($R > 0.85$), so to simplify analyses, and because it explained the greatest variation in response variables, I used mean percentage of bed moved in the year prior (approximately disturbance magnitude).

**Benthic communities**

Benthic communities were sampled on four occasions (April, September, and December 1999 and February 2000), with macroinvertebrates and periphyton collected from five cobbles-sized stones selected using a random grid. Stones were chosen as sampling units so that samples reflected those organisms directly associated with surfaces where periphyton communities developed. Stone sampling produces higher density estimates than other methods (Taylor et al. 2001), but focuses on habitats where herbivores are concentrated. Stones were lifted into a triangular-shaped kick net (300-μm mesh) placed downstream, rinsed, invertebrates were preserved in 80% ethanol, and stones were frozen.

In the laboratory, stones were thawed, periphyton was removed from upper surfaces with a toothbrush and filtered onto pre-ashed Watman GF/C glass fiber filters, dried for 24 h at 65°C, weighed to the nearest 0.1 mg, ashed at 450°C for 1 h, and reweighed to enable calculation of biofilm ash-free dry mass (AFDM). Stone surface area was determined by wrapping stones in aluminum foil and using a weight to area.
Table 1. Location, physicochemical conditions, and fish communities at 20 sites on 18 streams in the Cass-Cragieburn Basin of the upper Waimakariri River, South Island, New Zealand. Physicochemical characteristics are the average of measurements made at the time of electrofishing samples (n = 2 in most cases). Current velocity was estimated by the passage of dye through the site, depths and widths were averaged from three transects, substratum D50 is the median substrate size from measures of the longest axis of 100 particles selected randomly, and conductivity was measured with a handheld meter. Fish communities are the average of all electrofishing samples during the study at a site and include brown and rainbow trout (salmonid biomass) as a percentage of total fish biomass. Dashes (-) indicate situations where fish were absent.

| Site name (*unofficial)     | Grid reference (NZ map grid) | Altitude (m) | Current velocity (m s⁻¹) | Depth (cm) | Width (m) | Canopy cover (%) | Substratum D50 (cm) | Conductivity (μs cm⁻¹ @ 25°C) | Fish biomass (g m⁻²) | Salmonid biomass (%) |
|-----------------------------|------------------------------|--------------|--------------------------|------------|------------|------------------|---------------------|-----------------------------|---------------------|---------------------|
| Bradley stream*             | 2405604E, 5777728N           | 730          | 0.41                     | 9          | 1.3        | 0                | 10                  | 111                         | 8.76                | 0                   |
| Cass River                  | 2408038E, 5797082N           | 570          | 1.67                     | 22         | 3.8        | 0                | 8                   | 46                          | 0.37                | 0                   |
| Cass spring*                | 2408163E, 5797082N           | 550          | 0.64                     | 9          | 1.4        | 0                | 3                   | 51                          | 4.20                | 2                   |
| Cave stream (Lyndon)        | 2405188E, 5783479N           | 870          | 0.51                     | 13         | 2.2        | 50               | 11                  | 46                          | 2.02                | 85                  |
| Cave stream (picnic)        | 2406704E, 5783389N           | 805          | 0.69                     | 17         | 2.8        | 10               | 9                   | 54                          | 3.20                | 100                 |
| Coach stream                | 2409200E, 5765991N           | 770          | 0.58                     | 18         | 1.4        | 10               | 8                   | 93                          | 3.67                | 0                   |
| Cragieburn                  | 2408294E, 5784520N           | 690          | 0.94                     | 23         | 6.7        | 0                | 12                  | 38                          | 4.23                | 92                  |
| Cutting stream*             | 2407704E, 5783590N           | 830          | 0.27                     | 6          | 0.9        | 40               | 7                   | 49                          | 0.00                | -                   |
| Grasmere stream             | 2408793E, 5796332N           | 570          | 1.14                     | 35         | 3.0        | 0                | 8                   | 76                          | 3.99                | 12                  |
| Kowai River                 | 2411250E, 5764476N           | 590          | 1.50                     | 15         | 2.5        | 0                | 6                   | 55                          | 0.71                | 0                   |
| Manson Creek                | 2409454E, 5785355N           | 660          | 0.32                     | 4          | 0.5        | 0                | 10                  | 36                          | 5.69                | 80                  |
| Middle bush (upper)*        | 2409883E, 5796452N           | 640          | 0.90                     | 19         | 2.9        | 95               | 5                   | 106                         | 0.00                | -                   |
| Middle bush (lower)*        | 2408943E, 5796352N           | 580          | 0.42                     | 12         | 1.9        | 0                | 7                   | 101                         | 0.00                | -                   |
| Mt White Hut stream*        | 2422887E, 5795873N           | 605          | 0.27                     | 9          | 1.9        | 0                | 9                   | 70                          | 0.00                | -                   |
| Peacock stream*             | 2411703E, 5800874N           | 550          | 0.89                     | 22         | 2.4        | 80               | 5                   | 60                          | 5.16                | 94                  |
| Porter River                | 2406744E, 5772937N           | 920          | 0.69                     | 21         | 4.3        | 0                | 16                  | 45                          | 2.80                | 100                 |
| Slip spring*                | 2405139E, 5770962N           | 775          | 0.78                     | 18         | 2.8        | 0                | 8                   | 55                          | 1.94                | 98                  |
| Slovens stream              | 2416365E, 5789571N           | 575          | 0.52                     | 24         | 3.2        | 0                | 6                   | 77                          | 4.83                | 21                  |
| Thomas River                | 2404083E, 5777203N           | 745          | 0.50                     | 7          | 0.6        | 30               | 6                   | 62                          | 2.32                | 0                   |
| Whitewater River            | 2406374E, 5772927N           | 700          | 0.13                     | 21         | 7.7        | 0                | 12                  | 43                          | 0.87                | 43                  |
standard curve to estimate surface area. Large benthic biofilms in these streams are dominated by algae (including those in forest; Nyström et al. 2003), so even though biofilm AFDM can include heterotrophs and detritus, AFDM was indicative of benthic algal standing biomass.

Macroinvertebrates were counted and identified (mostly to genus; Winterbourn et al. 2000) and densities calculated based on upper stone surface areas.

To allow analysis of primary consumers relatively protected vs. unprotected from predatory fish, nonpredatory invertebrates were categorized according to shell or case presence offering increased protection (following Jellyman and McIntosh 2020). The presence of both types of consumers on stone tops during the April 1999 sampling was also recorded to evaluate differences in grazing behavior. This involved careful approach from downstream and counting visible invertebrates.

Prior to disturbance monitoring starting, all sites were electrofished during the 1997–1998 austral summer to measure fish abundance (as reported by McIntosh 2000). Most sites were electrofished again during the 1999–2000 summer. Fish biomass was calculated using the sum of the three passes since this best reflects biomass in situations where capture of large eels can violate depletion estimate assumptions (McIntosh 2000), and biomass was averaged over the two samples for analyses.

Statistical analyses
Interactive effects of disturbance and trout presence on algal AFDM were tested with generalized linear mixed effect model (GLMM) using a Gamma distribution and a log-link function with glmer in lme4 (Bates et al. 2015) using the drop1 function to assess significance using likelihood ratio tests. Influences on invertebrate communities were tested with linear mixed effect model (LMM) using lme in nlme (Pinheiro et al. 2020). These GLMM and LMM were based on a fully nested design incorporating mean proportion of the bed moved in the year prior (fixed covariate), trout presence or absence (fixed effect), site (random effect), and sample time (fixed effect nested within stream). I tested the effect of trout presence on the homogeneity of slopes of the relationship between disturbance and invertebrate communities by incorporating the interaction between trout and disturbance. Incorporating the stream sampled as a random effect meant that tests reflected that sites were replicates of trout effects. Modeled confidence internals (Fox and Weisberg 2019) were plotted in ggplot2 (Wickham 2016).

I also undertook quantile regression (Koenker 2020) to test for upper and lower limits in algal abundance along the disturbance gradient. This involved testing the performance of a linear function in defining 90th and 10th quantiles, with statistical significance of quantile slopes evaluated with bootstrapped standard errors of their coefficients and plotted as above.

Four components of invertebrate communities were examined in separate analyses. An angular transformation (arcsin square-root, “asq”) was applied to the mean proportion of bed moved, and log-transformations were used on the invertebrate community measures (except richness) to achieve normality and homogeneity of variance. To enable comparison of invertebrate taxon richness from samples contrasting markedly in abundance, richness was calculated by rarefaction (based on a sample size of 250 individuals 0.1 m²) using Primer 5.1. Original data are available on the University of Canterbury, Freshwater Ecology Research Group, Figshare (McIntosh 2022).

Results
Rivers varied hugely in flooding. The Cass and Kowai Rivers averaged more than 75% bed movement, with frequent events moving 100% of particles. In contrast, less than 2% bed movement occurred at Slip Spring and Slovens Stream (a spring and lake outlet, respectively).

This flood-related disturbance had a huge influence on fish (Table 1). Assemblages were dominated either by native galaxiids (Galaxias vulgaris or Galaxias paucispondylyus) or non-native salmonids (Salmo trutta and some Oncorhynchus mykiss), with occasional longfin eels (Anguilla dieffenbachii); all invertevores or piscivores. Total fish biomass was negatively associated with bed movement (R² = 0.47, F1,14 = 12.55, p < 0.01), with declines in all fish species but especially trout. Sites experiencing more than 40% bed movement contained low densities of galaxiids and, very importantly, trout were not recorded in these highly disturbed sites (Table 1). Thus, disturbance reduced overall abundance of predatory fish, and limited the regular occurrence of trout in the most disturbed rivers.

River algal biomass (AFDM) was not linearly associated (i.e., via a central response) with bed movement (or an interaction; Table 2a; Fig. 1). Moreover, there was no linear association between any invertebrate metric and algal biomass (all p > 0.3). However, there were patterns associated with fish. Although algal biomass averaged 0.44 ± 0.04 mg cm⁻² overall, it never rose above 0.4 mg cm⁻² (average ± SE: 0.18 ± 0.02 mg cm⁻²) in troutless rivers, whereas it ranged over three orders of magnitude in trout rivers, including some very high values (>1 mg cm⁻²). Thus, trout presence led to increases in algal biomass that were sometimes large, but any disturbance influence was nonlinear.

Although there was no linear central response between algal biomass and bed disturbance, rivers experiencing greater than 40% bed movement had consistently low algal biomass (mean ± 95% confidence interval [CI]: 0.18 ± 0.04 mg cm⁻²) and quantile regression indicated the presence of both lower- and upper-limit responses, the latter associated with trout. Firstly, the lower limit of algal abundance declined with bed disturbance, independent of fish, indicated by a significant
negative 10th quantile (Fig. 1). Secondly, a significant 90th quantile with a steep positive slope in trout streams indicated that the upper limit of algal abundance increased sharply with disturbance across the range of streams trout, as present in Fig. 1. No such limit was evident in streams lacking trout where algal biomass was consistently low (as described previously; Table 2a). Thus, streams with trout had higher algal abundance than those lacking trout, consistent with the expected trout-linked trophic cascade. However, maximum trout-associated cascade strength increased with disturbance until trout were no longer present.

Invertebrate assemblages on stones were substantially altered by disturbance, but also depended on trout presence. Firstly, taxon richness declined with disturbance in troutless rivers, whereas no effect of disturbance on taxon richness was detected in trout streams which spanned a smaller, more-benign, disturbance gradient (significant disturbance by trout interaction; Table 2b; Fig. 2a). Total invertebrate abundance declined substantially across the whole disturbance gradient, indicated by a significant main effect of disturbance and no significant interaction with trout (Table 2c; Fig. 2b). However, there was also a smaller main effect of trout whereby, for a given disturbance level, invertebrates were slightly more numerous in streams containing trout compared to those lacking trout (Table 2c; Fig. 2b).

These invertebrate abundance patterns were mainly driven by primary consumers protected with cases or shells, including cased conoesucid caddisfly larvae Pycnocentria and Pycnocentrodes, and the snail Potamopyrgus antipodarum. These protected consumers were more numerous than unprotected consumers in the stable half of the disturbance gradient and were significantly affected by both disturbance and trout (Table 2d). Protected consumer abundance declined sharply with disturbance, but at comparable levels of disturbance they

Table 2. Results of LMM evaluating the influences of trout presence (fixed effect), proportion of bed moved in the year prior (covariate), stream (random effect), and sample time (fixed effect, nested within stream) on (a) algal AFDM (b) rarefied invertebrate taxon richness, (c) total invertebrate abundance, (d) the abundance of primary consumers protected by cases or shells, and (e) the abundance of unprotected primary consumers (i.e., those lacking a case or shell). Bed movement was arctan-squareroot-transformed, and all invertebrate abundance measures and algal AFDM were log-e-transformed. Algal AFDM (a) was tested with likelihood ratio tests associated with a generalized mixed effects model, whereas (b)–(e) involved a LMM and F-ratio tests. Conditional and marginal pseudo-coefficients of determination for LMM (Rc_LMM2 and Rm_LMM2, respectively) are indicated.

| Numerator df | Denominator df | F-value | p       |
|--------------|----------------|---------|---------|
| (a) Algal AFDM (log_e[mg cm^-2]) | | | |
| Disturbance | 1 | - | 0.0004* | 0.98 |
| Trout | 1 | - | 7.00* | 0.008 |
| Date | 3 | - | 9.55* | 0.022 |
| (b) Invertebrate taxon richness (no./sample), Rc_LMM2 = 0.61, and Rm_LMM2 = 0.51 | | | |
| Disturbance | 1 | 53 | 38.20 | <0.001 |
| Trout | 1 | 18 | 0.0168 | 0.90 |
| Date | 3 | 53 | 4.476 | 0.007 |
| Disturbance × trout | 1 | 53 | 4.925 | 0.031 |
| (c) Total invertebrates (log_e[no./0.1 m^2]), Rc_LMM2 = 0.73, and Rm_LMM2 = 0.56 | | | |
| Disturbance | 1 | 54 | 42.45 | <0.001 |
| Trout | 1 | 18 | 6.043 | 0.024 |
| Date | 3 | 54 | 0.1387 | 0.94 |
| (d) Protected consumers (log_e[no./0.1 m^2]), Rc_LMM2 = 0.88, and Rm_LMM2 = 0.42 | | | |
| Disturbance | 1 | 54 | 6.126 | 0.017 |
| Trout | 1 | 18 | 9.741 | 0.006 |
| Date | 3 | 54 | 4.997 | 0.004 |
| (e) Unprotected consumers (log_e[no./0.1 m^2]), Rc_LMM2 = 0.60, and Rm_LMM2 = 0.22 | | | |
| Disturbance | 1 | 53 | 5.931 | 0.018 |
| Trout | 1 | 18 | 0.018 | 0.894 |
| Date | 3 | 53 | 0.649 | 0.587 |
| Disturbance × trout | 1 | 53 | 4.416 | 0.040 |

*Chi-square test statistic of a likelihood ratio test.
were more numerous in streams with trout compared to streams lacking trout (Fig. 2c).

Disturbance effects on unprotected consumers, mainly ubiquitous Deleatidium spp. mayflies, depended on an interaction with trout presence (Table 2e). Unprotected consumer abundance declined across the extensive troutless stream disturbance gradient, whereas disturbance did not significantly affect their abundance in trout streams (Fig. 2d). Overall, these patterns meant the composition of primary consumers differed in trout and troutless streams, and vulnerable consumers formed an increasing proportion of grazer assemblages as disturbance increased.

Observations of stone tops revealed strong effects of trout on daytime grazing activity of unprotected consumers. Comparing streams with <40% bed movement (where invertebrates were abundant enough to observe), there was an interaction between consumer type and trout presence affecting numbers observed (two-factor ANOVA on sqrt-transformed numbers; $F_{1,28} = 15.26$, $p < 0.001$). Unprotected and protected consumers were equally numerous on stone surfaces in troutless rivers (means ± SE: protected, 0.65 ± 1.4; unprotected, 1.9 ± 1.4 per stone), whereas in trout rivers protected consumers were much more numerous and almost no unprotected consumers were observed (protected, 4.12 ± 0.82; unprotected, 0.08 ± 0.82). Thus, there was potential for indirect effects of trout on algae to involve direct nonconsumptive effects of trout on unprotected herbivores that limited grazing.

**Discussion**

These results describe variable patterns in algal biomass which I infer reflect variations in the strength of trophic cascades; non-native trout were often, but not always, associated...
with increased algal abundance compared to similar rivers lacking trout. The cascade variability observed echoes the inconsistencies characterized in multiple within- and between-system comparisons (Shurin et al. 2002; Borer et al. 2005). By examining algal abundance across one of the largest conceivable ranges of disturbance, I have shown that predators and disturbance interact in nonlinear ways to affect cascade strength. Examining those patterns, especially in light of knowledge from previous experiments, reveals new information about control of cascade strength. In addition to dominance of nonconsumptive influences of predators and strong differences associated with a non-native compared to a native fish, the results point to disturbance: (1) resetting the stage for cascade occurrence by removing primary producers, (2) limiting top-down control by restricting the distribution of influential predators, and (3) modifying cascade drivers by altering herbivore composition through trait trade-offs.

Removal of primary producers, thereby resetting producer communities, was an obvious influence of disturbance. This resetting is consistent with assessments of bed movement influences on algal communities, whereby bed movement removes algal biomass and prevents the development of abundant periphyton communities (Biggs et al. 1999). These physical influences are similar to waves overwhelming top-down effects of urchins and otters on kelp forests by physically removing the kelp (Reed et al. 2011).

By restricting trout presence, flooding also limited the distribution of trout-driven cascades. Trout are seldom recorded in severely disturbed rivers, being excluded by habitat disruption and associated effects on their invertebrate food (Jellyman et al. 2013). This matches arguments for harsh abiotic regimes limiting biotic interactions by restricting the distribution of strong interactors like trout (Menge and Sutherland 1987), but cannot explain the increases in maximum cascade strength with disturbance in the stable half of the flooding gradient.

In streams where trout was present, the maximum algal abundance was positively correlated with disturbance. Both Peckarsky et al. (2015) and Biggs et al. (1999) observed similar algal increases with disturbance in trout streams along the stable portion of flood-disturbance gradients. These patterns are likely associated with trait trade-offs between vulnerability to predation and disturbance affecting the composition of macroinvertebrate primary consumers and their subsequent vulnerability to predators. Invertebrates protected with cases or shells are less vulnerable to predation by drift-feeding predatory fish, but compared to mobile invertebrates lacking such protection are more vulnerable to rock-rolling disturbances (Wootton et al. 1996; Power et al. 2008). Thus, as bed-moving disturbance increases, grazer composition changes from a well-protected set of herbivores largely unaffected by predators to mobile herbivores better able to cope with floods, but more vulnerable to predators (Jellyman and McIntosh 2020). This is the same mechanism driving interannual variability in grazer composition in Northern Californian streams (Power et al. 2008) and grazer composition across a flooding gradient in Rocky Mountain streams (Peckarsky et al. 2015). This increasing vulnerability of macroinvertebrate herbivores to predatory fish as disturbance rises likely provides the potential for trophic cascade strength to increase with disturbance.

The potential for trout to have the strong trophic effects does not explain the inconsistency though. The variable pattern is typical of the nonlinear dynamics associated with trophic cascades from lakes (Rogers et al. 2020), and it is characteristic of situations where multiple interacting processes drive responses. I can only speculate on the cause of this inconsistency, but it may involve the opening of “windows of opportunity” for rapid algal growth, especially in spring, or temporal variation in the supply of terrestrial subsidies to the aquatic system (Nakano and Murakami 2001).

The variations in cascade strength revealed here also highlight the value of focusing on spatial and temporal changes. Herbivores are more vulnerable to top-down forces following disturbance (Wootton et al. 1996; Power et al. 2008; Spiller et al. 2018), and this is consistent with changes in cascade strength being linked to alterations in consumer traits (Rogers et al. 2020). Spiller et al. (2018), for example, liken the periods following disturbance to “herbivore free time” and link stronger top-down control following hurricanes on Bahamian islands with periods when more vulnerable species are in the majority. This contrasts suggestions that strength of biotic interactions will weaken with disturbance as simple models propose (Menge and Sutherland 1987). Overall, much evidence now suggests that trophic interactions can range from very strong to completely absent, and can even reverse depending on conditions, so should not be regarded as static (Marcarelli et al. 2020). My results show a more nuanced understanding of how the strength of these interactions changes will emerge from increased focus on disturbance effects on the traits of herbivores and predators.

The range trophic patterns observed was only revealed by sampling across a wide disturbance gradient over multiple seasons. This observational approach’s disadvantages include inferring rather than directly measuring cascade strength, but previous experiments provide confidence that the patterns observed, including the prevalence of nonconsumptive effects (McIntosh and Townsend 1996), were caused by a combination of trout and disturbance. Firstly, that unprotected consumers were much less numerous on stone tops in trout compared to troutless streams indicates that trout-driven cascades involved restrictions on herbivore grazing activities as expected (Flecker and Townsend 1994; McIntosh and Townsend 1996). Secondly, non-native trout typically have much stronger top-down interaction strengths than native galaxiids (Flecker and Townsend 1994; McIntosh and Townsend 1996; Nyström and McIntosh 2003). And finally, that by changing the composition of consumers, disturbance can substantially alter the outcome of trophic interactions (Nyström and McIntosh 2003; Jellyman and McIntosh 2020).
My findings add to an already burgeoning literature describing the details of controls on trophic cascades, but they also shed new light on an important driver, disturbance, that is set to become ever more influential with climate warming (Milly et al. 2005). The role of disturbance in modifying trophic control, especially in setting the stage for stronger top-down interactions, is noteworthy. It challenges the view that disturbance decreases the strength of top-down control. It is also particularly significant because climate warming is quickly modifying disturbance regimes.

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