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Effects of Disturbance on River Food Webs

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colonization between censuses) was 0.45% for dry prairies, 0.77% for mesic prairies, and 1.03% for wet prairies. These values imply that half the plant species present in a remnant wet prairie would disappear in less than a half-century, whereas, in the best case, half the botanical diversity of a remnant dry prairie would disappear in slightly more than a century. Much of this loss involves short plants; species <0.5 m tall account for 52, 42, and 41% of the absolute loss in dry, mesic, and wet prairies, respectively. N-fixers account for 11% of the absolute loss and have 45% less recruitment than non-fixers. Losses among regionally rare species were especially severe; the 13 state-listed endangered or state-listed threatened species in our remnants lost 28 of 38 total occurrences, an absolute loss of 74%, more than twice the average of 34% for all species.

The implications of our findings for conservation are clear. First, it is essential to burn existing prairie remnants to help offset loss of ignition sources due to disruption of landscape context and human cultural practices. Prescribed burns should be conducted over a small portion of each remnant in any single year so that fire-sensitive organisms (for example, certain insects and lizards) are not extirpated. Second, conservation efforts should focus on species that are short, small-seeded, N-fixing, regionally rare, or possess a combination of these traits, especially on mesic to wet sites. Third, local plant extinctions are proceeding at such a high rate (0.5 to 1.0% per annum) that several taxa are in danger of being lost from the landscape. Of 266 species originally found across 54 sites in the 1940s and 1950s, only 228 persisted until the late 1980s, which represents an absolute loss of 14.3% of all native plant species. Although such species are not restricted to prairie remnants, often they are most common there, which suggests that the observed losses reflect a broad regional process.

The interruption of the landscape-scale process of wildfire may be eroding biodiversity in many habitats worldwide. The composition, structure, dynamics, and productivity of several ecosystems—taiga, temperate forests and grasslands, Mediterranean scrub, savannas, and even some wet tropical forests—are strongly affected by fire; many of their species require fire to persist or reproduce (1, 13–15, 28). The mechanism underlying local plant extinction we propose for prairies may operate in many other fragmented communities and thus have broad ramifications for conservation and ecosystem management.

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29. This research was supported in part by NSF grant DEB-9107379 to T.J.G., and by a grant from the Friends of the University of Wisconsin Arboretum to T.J.G. and M.K.L. Fieldwork by M.K.L. was supported, in part, by a Hatch grant to J. Harrington. We thank R. May, D. Tilman, and D. Waller for their comments on an early draft.

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## Effects of Disturbance on River Food Webs

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A multitrophic model integrating the effects of flooding disturbance and food web interactions in rivers predicted that removing floods would cause increases of predator-resistant grazing insects, which would divert energy away from the food chain leading to predatory fish. Experimental manipulations of predator-resistant grazers and top predators, and large-scale comparisons of regulated and unregulated rivers, verified the model predictions. Thus, multitrophic models can successfully synthesize a variety of ecological processes, and conservation programs may benefit by taking a food web perspective instead of concentrating on a single species.

Although conservation programs typically concentrate on the direct impacts of environmental change on a single species, ecological experiments and theory demonstrate that species are affected in complex ways by other species, ecosystem productivity, and disturbance regimes (1–4). Therefore, to

understand and predict the consequences of impacts on the environment, ecologists must shift from an autecological perspective to consideration of the interaction of multiple causal factors. For example, changes in climate, land use, and water regulation or diversion all may alter the flooding regime

of rivers. How do changes in flooding disturbance affect species in river food webs? Successfully predicting the answer to this question requires a framework that can synthesize the direct effect of disturbance-induced mortality, as well as the indirect compensatory or reinforcing effects of interactions among various species in an ecological community.

Multitrophic dynamic models of species interactions provide a potentially useful synthetic theoretical framework to simultaneously examine a variety of ecological processes (1, 2). Within this framework, species interactions are modeled explicitly, and the dynamics of limiting resources can be treated as species at the bottom of the food web. Disturbance can be incorporated by adding density-independent mortality terms to the dynamics of each species. In previous studies of rivers in northern California, we have shown that such a framework can predict the consequences of removing top predators from a food web and of varying productivity at the base of the food web (1, 3). Here, we consider whether the effects of disturbance can also be incorporated into such a theoretical framework.

Our observations of free-flowing rivers in northern California during the droughts of 1990–1992 and 1994, when scouring floods typical of the winter rainy season were absent or reduced, indicated that flood disturbance can have important effects on river food webs. In the absence of floods, we observed a marked increase in a predator-resistant caddisfly, *Dicosmoecus gilvipes* (5). The combined effect of large size and robust protective cases effectively eliminates predation on this species by most fish and invertebrate predators, but these same traits can make it susceptible to flood mortality (6). Its heavy protective case restricts *Dicosmoecus* to the river bottom, and its large size renders most interstitial spaces ineffective as refuges from mortality. As a result, *Dicosmoecus* has difficulty avoiding rolling rocks during scouring floods. Moreover, attaining large size requires longer aquatic larval periods than those of smaller grazers such as midges (Chironomidae) or mayflies (Ephemeroptera), which increases the time during which *Dicosmoecus* is at risk of flood-induced mortality. Two important observations further support this inference of a tradeoff between resistance to flood disturbance and resistance to predation: *Dicosmoecus* densities in April 1992 showed a 77%

reduction [from  $82.3 \pm 65.4$  (SD) to  $18.8 \pm 23.6$  individuals per square meter] after a brief spate, and no consumption of *Dicosmoecus* occurred in feeding trials using a range of predators (7).

These observations indicated that a reasonable multitrophic model of this river system might consist of two linked food chains, one going from algae to predator-susceptible grazers to predatory fish and insects and the other going from algae to predator-resistant grazers. Such a situation can be modeled as

$$dA/dt = b_a A L e^{-c_a A} - c_h H A - c_d D A - m_a A$$

$$dH/dt = b_h c_h A H - c_p P H - m_h H$$

$$dP/dt = b_p c_p H P - m_p P$$

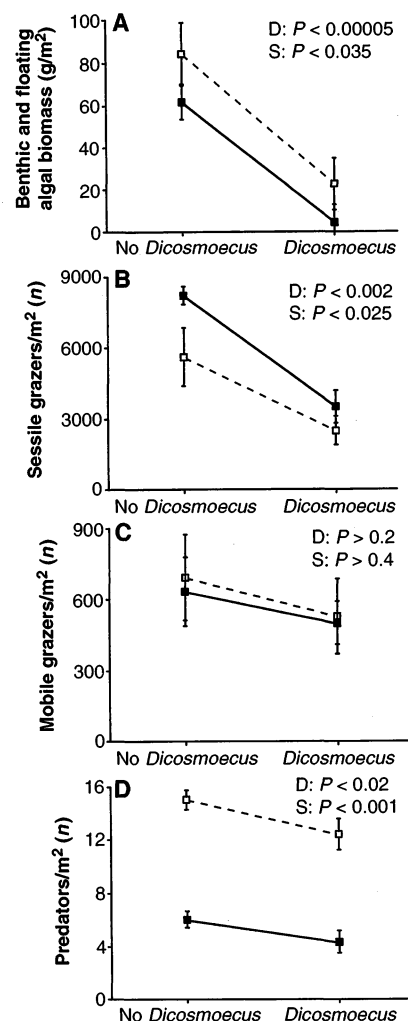
$$dD/dt = b_d c_d A D - m_d D \quad (1)$$

where  $A$ ,  $H$ ,  $D$ , and  $P$  are the abundances of algae, predator-susceptible herbivores, predators, and predator-resistant grazers (*Dicosmoecus*), respectively;  $L$  is the amount of incident light available for algae to convert into new offspring by photosynthesis (1);  $b_x$  (where  $x$  is  $a$ ,  $h$ ,  $d$ , or  $p$ ) is the conversion efficiency of consumed resource into individuals of species  $x$ ;  $c_x$  is the per capita consumption rate of resources by species  $x$ ;  $e$  is the base of the natural logarithm; and  $m_x$  is the density-independent mortality (due to disturbance or other causes) experienced by species  $x$ .

Solved at steady state, this multitrophic model makes predictions about the average consequences of reducing disturbance (decreasing  $m_x$ ), given that disturbance increases the mortality of predator-resistant grazers more than that of predator-susceptible grazers. In short, disturbance reduction is predicted to diminish energy flow in the food chain leading to predatory fish, diverting most of the ecosystem energy to predator-resistant grazers. First, reduction of flooding disturbance should increase predator-resistant grazers because of a direct reduction in mortality. Second, removal of disturbance should indirectly decrease algal abundance because of increases in grazing pressure. Third, reduced flooding should indirectly decrease predator abundance because less energy becomes available to the longer food chain. Finally, predator-susceptible grazers should neither increase nor decrease, despite the change in the abundance of their competitors, because decreases in population growth rate arising from lower algal crops are ultimately offset by lower predator populations. This last prediction has interesting implications for recent experimental investigations focusing on whether pairs of species compete (8), because it indicates that the existence of competition may be underestimated when

interactions among the larger community are ignored.

To test the predictions of the model, we experimentally manipulated the abundance of *Dicosmoecus* in mesocosms placed in the South Fork Eel River on the Angelo Coast Range Preserve, Mendocino County, California (1, 3, 6). We constructed in-stream channels (1.56 m by 1.17 m by 0.78 m) of wooden frames, clear plastic sides, and ends and bottom of plastic screen (6-mm mesh). Twenty-four channels were placed in blocks of four in six similar reaches in the river, and river gravel was added to each channel to a depth of 5 cm. We also added eight ceramic tiles (7.5 by 7.5 cm) to the bottom



**Fig. 1.** Mean ( $\pm 1$  SE) block-adjusted responses of (A) algal biomass, (B) sessile predator-susceptible grazers, (C) mobile predator-susceptible grazers, and (D) small predators to the manipulation of the predator-resistant grazer *Dicosmoecus gilvipes* (D) and the top predator *Onchorynchus mykiss* (steelhead; S). Lines indicate treatments with steelhead present (—) and absent (---). Probabilities were generated from one-sided  $t$  tests used to test the directional predictions of the model.

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of each channel to serve as uniform sampling substrates (1). On 24 June 1992, we introduced 120 *Dicosmoecus* into each of two randomly chosen channels in each block. Additionally, we crossed each treatment with an additional treatment, the presence or absence of three juvenile steelhead (*Oncorhynchus mykiss*, 40 to 80 mm standard length), to test several other model predictions: The addition of steelhead

(which increases mortality of small fish and predatory invertebrates) should reduce small predators, increase predator-susceptible grazing insects, and reduce algal cover. We censused the channels on 24 July 1992, just before *Dicosmoecus* diapause (9).

As predicted, manipulating *Dicosmoecus* and steelhead caused significant changes in community structure [multivariate analysis of variance (MANOVA),  $P < 0.0002$  for *Dicosmoecus* treatment,  $P < 0.00005$  for steelhead treatment,  $P > 0.45$  for interaction of *Dicosmoecus* and steelhead, and  $P > 0.1$  for location effect] (Fig. 1). Adding *Dicosmoecus* caused significant ( $P < 0.05$ ) declines in algal biomass ( $-83\%$ ), predator abundance ( $-23\%$ ), and sessile grazer abundance (midges and the caddisfly *Tinodes* sp.;  $-56\%$ ), but not in mobile grazer abundance; whereas adding steelhead caused significant declines in predator abundance ( $-62\%$ ) and algal biomass ( $-54\%$ ), as well as significant increases in sessile grazer abundance ( $43\%$ ), but no change in mobile grazer abundance. The trophic level-specific predictions of the model were supported for all changes except the decline in sessile insect abundance in the presence of *Dicosmoecus*.

The unanticipated response of sessile insects to *Dicosmoecus* appeared to arise from two factors. First, *Dicosmoecus* appeared to prey on sessile insect larvae, and *Dicosmoecus* feeding activity destroyed protective tubes and prevented establishment of sessile insects on the substrate. Second, the increase in algae in the absence of *Dicosmoecus* provided a physical substrate in which insects could hide (10). Although adding *Dicosmoecus* predation on midges into the model does not result in the decline of other grazers, destroying protective tubes and reducing algal cover modifies the interaction between predators and their prey (11), which increases predation intensity on grazers. A model that includes this type of indirect interaction predicts all of the patterns arising in the experimental results.

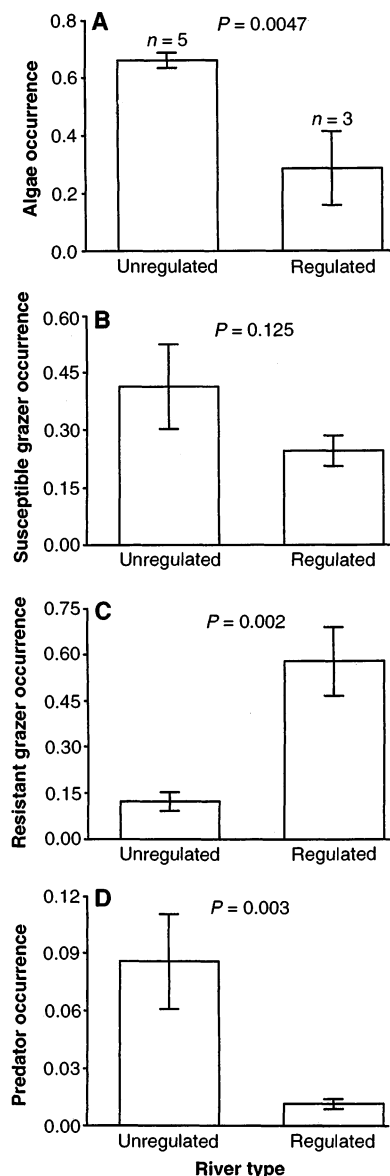
To determine whether the predictions of the model could be generalized beyond our experimental channels, we compared surveys of the biota of unregulated (regularly flooding) and regulated (flooding prevented) rivers in northern California (12). As predicted by the model and experimental results, the regulated rivers we surveyed exhibited a significantly higher occurrence of predator-resistant grazers ( $369\%$ ), a significantly lower occurrence of algae ( $-58\%$ ) and predators ( $-87\%$ ), and a slightly, but not significantly, lower occurrence of predator-susceptible grazers ( $-41\%$ ), relative to the rivers with natural flows we surveyed (Fig. 2).

Our results have several implications for

both basic and applied issues. From a basic perspective, our results demonstrate that multitrophic models can provide a useful framework to synthesize multispecies interactions and disturbance regimes, and thus may provide one approach for understanding the role of disturbance in complex natural ecosystems. From an applied perspective, our results emphasize the need to shift from a single-population perspective to a community or food web perspective when developing strategies for resource management or conservation. For example, there has been an alarming decline in salmonid populations along the Pacific coast of North America, and the regulation of rivers through damming has been strongly implicated as one major cause (13, 14). Managers trying to remedy this situation have concentrated on the possible direct effects of dams on salmonids, for example, in preventing spawning migrations or grinding up juveniles in turbines, and have consequently recommended autecological solutions. By taking a food-web approach, our results demonstrate that such strategies may be insufficient because, in the absence of scouring floods, the food web beneath the fish collapses. Therefore, although mitigation of direct effects of dams on fish may be important, alternative approaches such as pulsed water releases to create riverbed scouring may be required to restore food web integrity, as well as to address other impacts related to river geomorphology (14, 15).

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**Fig. 2.** Average ( $\pm 1$  SE) occurrence (percentage of transect sites with a given trophic group) during the summer growing season of (A) visibly conspicuous algae (filamentous diatoms, *Oscillatoria*, *Rivularia*, *Nostoc*, *Cladophora*, *Oedogonium*, and *Zygnematales*), (B) predator-susceptible grazers, (C) predator-resistant grazers, and (D) predators in unregulated (with flood disturbance) and regulated rivers (flood disturbance greatly reduced) in northern California. Probabilities were generated from one-sided  $t$  tests used to test the directional predictions of the model.

rissia and *Physella* (Pulmonata); and *Eubianix* (Psephenidae)], except for midge (Chironomidae) larvae, on the top and bottom of each tile. Midges were counted on only one tile because of their high abundance. We collected benthic algae (largely a mixture of *Cladophora glomerata*, *Nostoc* spp., and *Epithemia* spp.) from one randomly selected tile in each treatment by scraping the tile with a razor blade and measuring ash-free dry weight in the laboratory. All floating algal mats in a channel were collected with an aquarium net, spun in a salad spinner for a standard 50 turns to remove excess water, and weighed. Subsamples of floating algae were collected, dried, weighed, and analyzed through measurement of ash-free dry weight to calibrate wet mass with ash-free dry weight. We used a blocked, two-way MANOVA to test for community-wide differences among treatments,

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## Appetite-Suppressing Effects of Urocortin, a CRF-Related Neuropeptide

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The neuropeptide corticotropin-releasing factor (CRF) is well known to act on the central nervous system in ways that mimic stress and result in decreases in exploration, increases in sympathetic activity, decreases in parasympathetic outflow, and decreases in appetitive behavior. Urocortin, a neuropeptide related to CRF, binds with high affinity to the CRF<sub>2</sub> receptor, is more potent than CRF in suppressing appetite, but is less potent than CRF in producing anxiety-like effects and activation. Doses as low as 10 nanograms injected intracerebroventricularly were effective in decreasing food intake in food-deprived and free-feeding rats. These results suggest that urocortin may be an endogenous CRF-like factor in the brain responsible for the effects of stress on appetite.

Corticotropin-releasing factor, a neuropeptide isolated from the mammalian brain (1), has been implicated in the mediation of the integrated physiological response to stress (2, 3). When released from the median eminence into the hypophyseal portal system, CRF exerts powerful effects to stimulate the release of adrenocorticotrophic hormone (ACTH) from the pituitary; thus, as a hypothalamic-releasing factor, CRF regulates glucocorticoid responses to stress (2). When infused within the central nervous system, CRF mimics most of the behavioral responses to stress (3). Central administration of CRF increases arousal, as measured by changes in cardiovascular parameters (4) and locomotor activity (5), and, like stress, produces "anxiogenic-like" and anorectic effects in a variety of behavioral paradigms (3, 6). These effects are largely independent

of the activation of ACTH and corticoids (7), suggesting a direct action on brain CRF receptors implicated in behavioral responses to stressors. Until recently, only one endogenous CRF had been isolated from the mammalian brain, suggesting that only CRF itself was directly involved in stress-induced behavioral changes, including anorexia. However, the identification in the mammalian brain of another neuropeptide of the CRF family, urocortin (UCN) (8),

has reopened the question, suggesting a potential physiological role for endogenous UCN in activating central CRF receptors.

The major cellular sites of expression of UCN in the rat brain were detected in the Edinger-Westphal nucleus, the lateral superior olive, the lateral hypothalamus, and the supraoptic nucleus, all regions that do not contain CRF mRNA (8). Binding studies have shown that UCN binds with very high affinity to both the identified CRF receptors, CRF<sub>1</sub> (9) and CRF<sub>2</sub> (10), but has a much higher affinity for the CRF<sub>2</sub> receptor than CRF, and the distribution of UCN fibers correlates well with the distribution of the CRF<sub>2</sub> receptor but not the CRF<sub>1</sub> receptor (8). These observations led to the hypothesis that central infusion of UCN may produce behavioral effects that only partially overlap with those produced by CRF. To test this hypothesis, we analyzed the effects of a wide range of concentrations of UCN, urotensin I, and r-h CRF (0.01 to 10.0 µg per animal) after they were infused into the cerebral ventricle (ICV) of rats previously implanted with intracerebroventricular cannulas.

Rats were food-deprived for 24 hours and food consumption was tested for 2 hours after ICV injection of vehicle or different doses of the peptide. UCN con-

**Table 1.** Effect of central and peripheral administration of urocortin on mean blood pressure. Data are represented as mean ± SEM (*n* = 5). Changes in mean arterial blood pressure (ΔMAP) were calculated as the difference between the basal values taken before urocortin administration. Mild hypertensive effects were obtained after central injection, whereas peripheral administration exerted prolonged hypotensive effects. No significant change in myocardial contractility was recorded after central administration (22). Data were analyzed by using analysis of variance (ANOVA) followed by Tukey's test. ICV, intracerebroventricular; SC, subcutaneous.

Urocortin dose (µg)	Time course of ΔMAP (mm Hg)		
	30 min	60 min	90 min
Central (ICV) administration			
0	-0.9 ± 0.04	1.5 ± 0.02	0.8 ± 0.11
1.0	6.9 ± 2.50	0.8 ± 0.12	0.2 ± 0.05
10.0	12.2 ± 1.32*	6.3 ± 0.15	1.8 ± 0.14
Peripheral (SC) administration			
0	1.5 ± 0.04	1.2 ± 0.02	-0.8 ± 0.15
10.0	-17.8 ± 1.44*†	-26.7 ± 2.31*†	-32.7 ± 2.61*†

\**P* < 0.01 versus vehicle; †*P* < 0.01 versus central administration, at the same urocortin dose.

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