



Food web rewiring drives long-term compositional differences and late-disturbance interactions at the community level

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Ecological communities are constantly exposed to multiple natural and anthropogenic disturbances. Multivariate composition (if recovered) has been found to need significantly more time to be regained after pulsed disturbance compared to univariate diversity metrics and functional endpoints. However, the mechanisms driving the different recovery times of communities to single and multiple disturbances remain unexplored. Here, we apply quantitative ecological network analyses to try to elucidate the mechanisms driving long-term community-composition dissimilarity and late-stage disturbance interactions at the community level. For this, we evaluate the effects of two pesticides, nutrient enrichment, and their interactions in outdoor mesocosms containing a complex freshwater community. We found changes in interactions strength to be strongly related to compositional changes and identified postdisturbance interaction-strength rewiring to be responsible for most of the observed compositional changes. Additionally, we found pesticide interactions to be significant in the long term only when both interaction strength and food-web architecture are reshaped by the disturbances. We suggest that quantitative network analysis has the potential to unveil ecological processes that prevent long-term community recovery.

multiple disturbances | food web | community ecology | recovery | composition

Multiple disturbances arising from anthropogenic activities may modify the composition and functioning of ecological communities (1). A recent meta-analysis on the effects of pulse disturbances on aquatic and terrestrial communities has revealed that functional and compositional responses to pulse disturbance are substantially different (2). After a pulse disturbance, the function a community performs (typically measured as biomass) is usually recovered within a relatively short time frame, whereas community composition takes longer to recover. Moreover, in many cases, perturbed communities by pulse disturbances tend to differ further from the unperturbed ones as time passes (2). Such lack of compositional recovery is only evidenced by using multivariate metrics (e.g., Bray–Curtis dissimilarity or ordination techniques), which account not only for changes in species number, but also for species identities and relative abundances (3). Univariate descriptors of composition, such as diversity indices, evenness, and dominance, however, do not reflect such changes in community composition (2), suggesting that species reordering after pulsed disturbance is a common phenomenon (1). Despite this being consistently reported in many experiments across ecosystems (4) and different types and numbers of disturbances applied (1), the mechanism(s) driving such species reorganization in multitrophic communities are anything but clear.

Recently, a new framework trying to explain the mismatch between multivariate composition and univariate functional and diversity descriptors has been proposed (5). This approach links univariate and multivariate statistical techniques using rank abundance curves, which describe dynamic species-level community changes. Despite this being a stepping stone to the understanding of disturbance impacts at the community level, this approach provides little information on the direct and indirect mechanisms driving community changes, particularly in multitrophic communities, where species interactions may modify the overall effects of disturbance (6).

The situation complicates when one tries to assess the effects of co-occurring disturbances on communities and ecosystems. At present, several syntheses have focused on summarizing multiple-disturbances effects in different ecosystems (7–9) and in proposing methods to classify interactions between disturbances (9–11), while the temporality of disturbance effects has received little attention (but see refs. 12 and 13).

Interactions between disturbances are temporal scale-dependent (14). That is, significant effects of multiple disturbances may appear only at a later stage, usually after cessation of pulsed perturbation. Time-dependent interactions between disturbances have been reported across different levels of biological organization, ranging from individuals (13) to communities (15) and ecosystem properties (14). Recently, rapid evolution and

Significance

Multiple anthropogenic disturbances affect the structure and functioning of communities. Recent evidence highlighted that, after pulse disturbance, the functioning a community performs may be recovered fast due to functional redundancy, whereas community multivariate composition needs a longer time. Yet, the mechanisms that drive the different community recovery times have not been quantified empirically. We use quantitative food-web analysis to assess the influence of species interactions on community recovery. We found species-interactions strength to be the main mechanism driving differences between structural and functional recovery. Additionally, we show that interactions between multiple disturbances appear in the long term only when both species-interaction strength and food-web architecture change significantly.

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adaptation have been proposed as mechanisms underpinning the late appearance of synergistic responses at the population level (16). However, we still lack suitable approaches to understand what processes may be driving the (late) disturbance interactions at the community level.

In the last years, there has been a growing interest in assessing how species interactions drive community and ecosystem responses to single and multiple disturbances (17–20). Disturbance-driven changes in abundance in one trophic level or in a population may alter the structure of the complex network, in which species are embedded by means of its interactions (21, 22). These disturbances can modify the structural properties of the food web, such as the number and configuration of interactions, as well as the biomass and energy fluxes, usually referred to as the interaction's strength (17, 23). Consequently, disturbance might affect food webs' topology (that is, who eats whom) by removal or addition of links, a concept known as topological rewiring. Alternatively, or in addition, disturbance might impact the strength of the food-web interactions (that is, the magnitude of the effect on the energy flow from one species to the other), which often result from changes in the consumptive demand of a consumer associated with shifts in the consumer's behavior, a concept known as interaction-strength rewiring (18, 22, 24). Potentially, the interaction-strength rewiring may prevent the recovery of the multivariate community composition without affecting the total number of species or community evenness (i.e., univariate descriptors and topological properties).

Here, we demonstrate how ecological network analysis may help in closing the gap between univariate and multivariate compositional descriptors of community composition by investigating the mechanisms underpinning disturbance effects at the community level. Specifically, we tested 1) whether there is a correlation between the relative change in community composition (e.g., Bray–Curtis dissimilarity) and the relative change in species-interactions strength; and 2) whether long-term compositional changes in communities caused by single pulse disturbances are reflected by changes in interactions strength. Finally, we investigated 3) whether the rewiring of interactions strength may be the driving mechanism causing the appearance of late interactions between disturbances.

For this, we used data from an outdoor mesocosm experiment, in which we evaluated the single and combined effects of two different pesticides, an herbicide (diuron) and an insecticide (chlorpyrifos), on freshwater communities over time under two nutrient scenarios (eutrophic and oligotrophic). The two pesticides were applied as single pulse disturbances, whereas nutrients were applied as press perturbation, starting 1 mo before the pesticides' application and being continuously applied throughout the experiment to simulate a eutrophic environment. We considered three periods representing the predisturbance situation (5 d before pesticide application), maximum-effect phase (15 d after pesticide application), and the expected-recovery phase (50 d after pesticide application). We chose those pesticides as they selectively target different compartments of the community. The pesticide concentrations used, despite being environmentally relevant (25, 26), were expected to affect 50% of the primary producers and consumers, respectively. Thus, changes in composition and in species interactions were projected to occur significantly. Moreover, the press (continuous) addition of nutrients and the consequent eutrophication was expected to reduce richness and to modify several topological parameters of the food web (17), allowing us to test pesticide interactions under two different environmental scenarios. Here, we combine unweighted or topological (without considering interaction strength) and quantitative (or

weighted) food-web properties to study the effects of single and multiple disturbances on community composition over time.

Results

Community Composition. Our study shows significant differences in community composition caused by the nutrients' enrichment in all three sampling days (permutational multivariate ANOVA [PERMANOVA], predisturbance: $F_{1,23} = 1.70$, $P = 0.022$; maximum effect: $F_{1,23} = 3.03$, $P = 0.003$; recovery: $F_{1,23} = 2.80$, $P = 0.001$; *SI Appendix, Table S2*). Both the herbicide and the insecticide shifted the community composition in the maximum-effect phase (PERMANOVA, herbicide: $F_{1,23} = 2.73$, $P = 0.003$; insecticide: $F_{1,23} = 6.75$, $P = 0.001$; *SI Appendix, Table S2*) and in the recovery phase (PERMANOVA, herbicide: $F_{1,23} = 1.88$, $P = 0.017$; insecticide: $F_{1,23} = 2.45$, $P = 0.002$; *SI Appendix, Table S2*). Interactions between pesticides were only significant in the recovery phase under noneutrophic conditions (PERMANOVA, $F_{1,23} = 2.26$, $P = 0.006$; *SI Appendix, Table S2*). Generally, we did not observe compositional recovery (Fig. 1). Communities undergoing different treatments were still well distinguished from the control in the multivariate space in the recovery phase, suggesting that different treatments promoted different long-term multivariate composition (2).

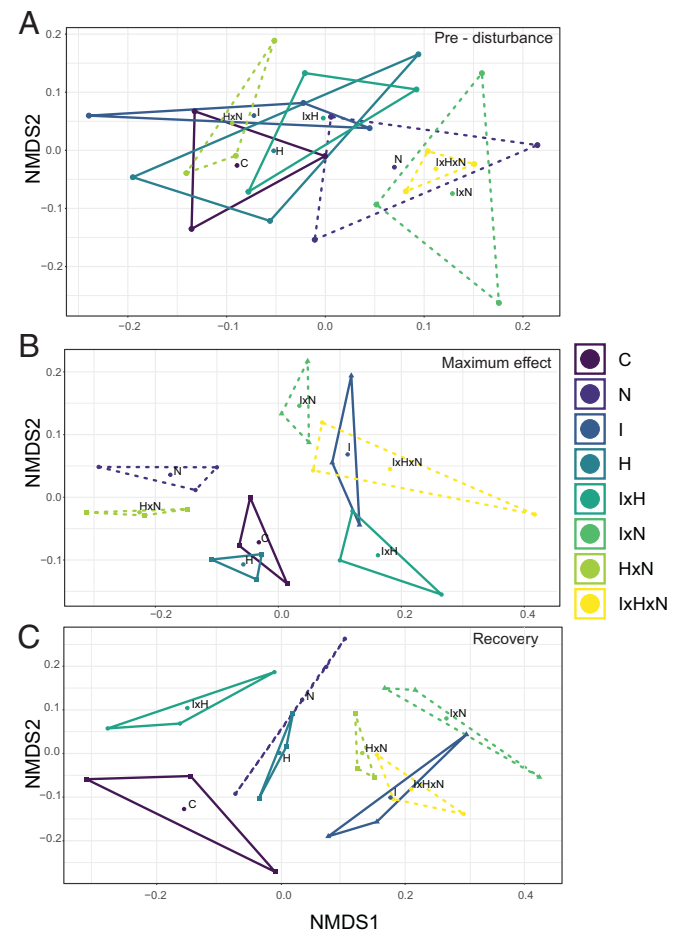


Fig. 1. NMDS of the community over time. NMDS plots show differences in community composition on the predisturbance phase (A), maximum-effect phase (B), and recovery phase (C). Treatments are defined by color, and eutrophic systems are characterized by a dashed line. The round dot in the middle of the three replicates of each treatment represents the centroid for the specific treatment. H, herbicide; I, insecticide; N, nutrients.

Species evenness was not significantly affected by the treatments ($P > 0.05$), whereas the Shannon's index was significantly reduced by the insecticide in the maximum-effect phase (ANOVA, $F_{1,16} = 6.05$, $P = 0.021$; *SI Appendix, Table S2*). Species richness was significantly reduced by the insecticide in the

maximum-effect phase (ANOVA, $F_{1,16} = 5.89$, $P = 0.027$; *SI Appendix, Table S2*) and by the nutrients in the maximum-effect phase (ANOVA, $F_{1,16} = 9.12$, $P = 0.008$; *SI Appendix, Table S2*) and recovery phase (ANOVA, $F_{1,16} = 26.49$, $P < 0.001$; *SI Appendix, Table S2*). Richness was also reduced by the

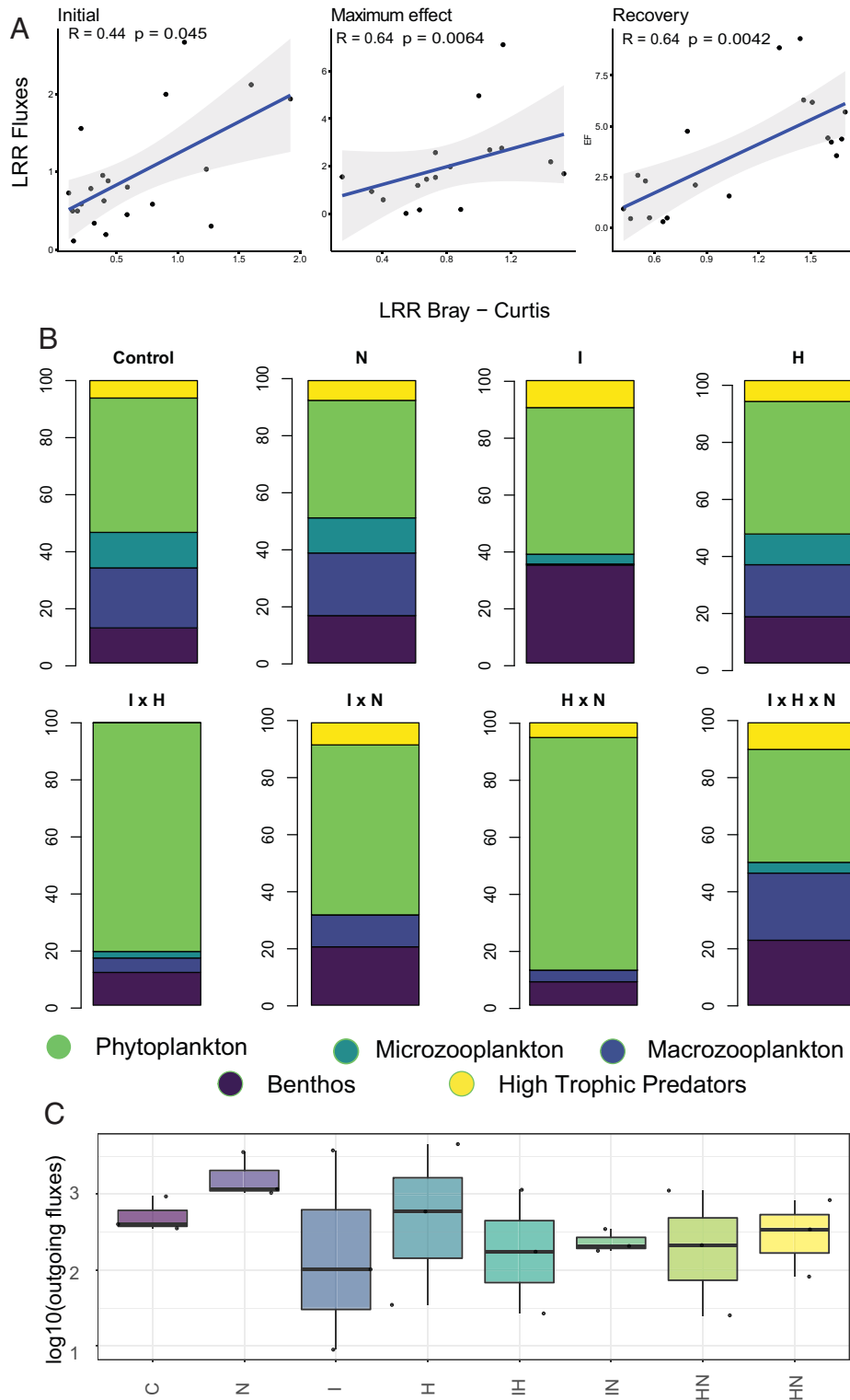


Fig. 2. Effects of stressors on the energy fluxes. (A) Spearman's rank correlation between the LRR of the energy fluxes and the LRR of the Bray-Curtis dissimilarity between the treatments and the control in each of the three experimental phases. The line represents the linear trend between the two variables, and the colored area represents the CI. (B) Visual representation of the proportional outgoing fluxes per trophic group in the different treatments in the recovery phase. The proportional outgoing fluxes were calculated by using the mean of the three replicates of each treatment. H, herbicide; I, insecticide; N, nutrients. (C) Box and whisker plots ($n = 3$, for all measures) of the total outgoing fluxes in the recovery phase. The center line indicates the median, while the bottom and top hinges of the box correspond to the 25th and 75th percentiles, respectively. Every replicate of each treatment is shown as an individual dot.

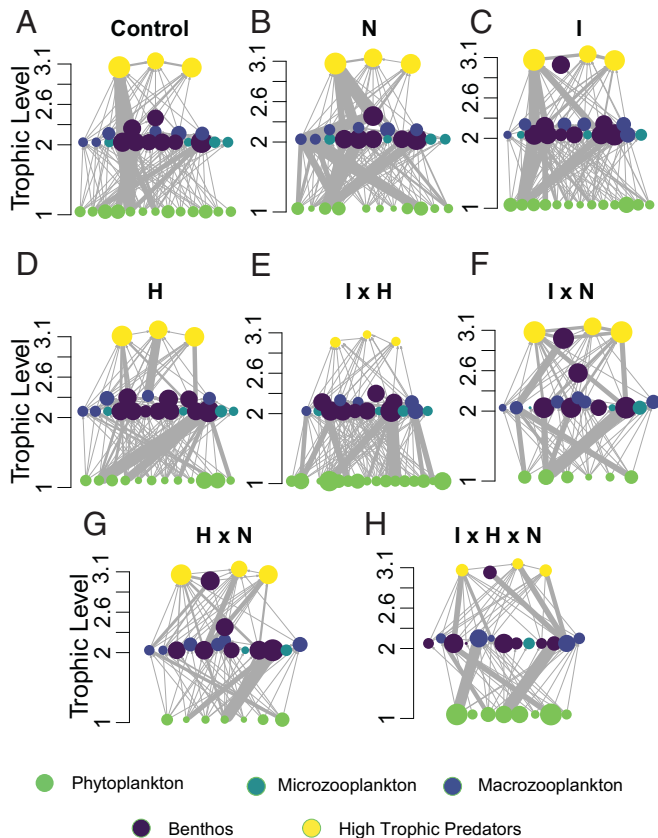


Fig. 3. Link-weighted representation of the trophic network in the recovery phase. The networks, weighted links, and nodes were built by using the average values of the fluxes and biomass of the three replicates per treatment. A shows the node and link weighted trophic network of the control replicates in the recovery phase; B that of the replicates treated with nutrients enrichment. C and D show the node and link weighted trophic networks of the replicates treated with the insecticide and the herbicide, respectively, in the recovery phase. E, F, G, and H show the node and link weighted trophic networks of the binary and tertiary interactions in the recovery phase, where H is the herbicide, I the insecticide, and N nutrients enrichment.

simultaneous application of the herbicide and the insecticide under noneutrophic conditions in the recovery phase (ANOVA, $F_{1,16} = 8.496$, $P = 0.010$; *SI Appendix, Table S2*).

Total biomass was significantly increased by nutrients enrichment in the predisturbance phase (ANOVA, $F_{1,16} = 2.24$, $P = 0.039$; *SI Appendix, Table S2*) and in the maximum-effect phase (ANOVA, $F_{1,16} = 7.12$, $P = 0.016$; *SI Appendix, Table S2*), while in the maximum-effect phase, the herbicide decreased the total community biomass (ANOVA, $F_{1,16} = 5.21$, $P = 0.038$; *SI Appendix, Table S2*).

Food-Web Properties. Unweighted topology-based food-web properties (number of links, link density, number of basal species, path length, generality, and vulnerability) were generally negatively influenced by nutrients enrichment in the maximum-effect and recovery phases (*SI Appendix, Table S3*). In the maximum-effect phase, also the insecticide significantly affected several food-web properties (*SI Appendix, Table S3*), while the herbicide did not. In the recovery phase, neither the insecticide nor the herbicide modified these metrics. Disturbances interactions on food-web properties appeared only in the recovery phase between the herbicide and the insecticide under noneutrophic conditions. The pesticide mixture significantly decreased the number of links (ANOVA, $F_{1,16} = 5.01$, $P = 0.039$), link density (ANOVA, $F_{1,16} = 3.12$, $P = 0.036$), and

generality (ANOVA, $F_{1,16} = 6.32$, $P = 0.023$) and increased the number of basal species (ANOVA, $F_{1,16} = 6.63$, $P = 0.020$).

Node-weighted properties were never modified by the insecticide, whereas the herbicide significantly decreased connectance in the maximum-effect phase (ANOVA, $F_{1,16} = 7.63$, $P = 0.037$; *SI Appendix, Table S4*). Nutrients' enrichment decreased connectance in the predisturbance phase (ANOVA, $F_{1,16} = 1.41$, $P = 0.036$) and generality and vulnerability in the recovery phase (ANOVA, $F_{1,16} = 9.56$, $P = 0.006$ and $F_{1,16} = 15.75$, $P = 0.001$, respectively). Significant interactions between disturbances were reported only in the recovery phase, when the mixture of pesticides (herbicide \times insecticide) significantly decreased connectance (ANOVA, $F_{1,16} = 5.14$, $P = 0.037$).

Link-weighted connectance was increased by the herbicide and nutrients as single treatments in the maximum-effect phase (ANOVA, $F_{1,16} = 11.18$, $P = 0.006$ and $F_{1,16} = 5.74$, $P = 0.029$, respectively; *SI Appendix, Table S5*) and by the herbicide as a single treatment in the recovery phase (ANOVA, $F_{1,16} = 4.46$, $P = 0.036$, respectively). Conversely, the insecticide and the mixture of the pesticides in the recovery phase decreased link-weighted connectance (ANOVA, insecticide: $F_{1,16} = 3.32$, $P = 0.048$ and insecticide \times herbicide: $F_{1,16} = 8.12$, $P = 0.011$). Link-weighted generality was increased by the nutrients in the predisturbance and recovery phase (ANOVA, $F_{1,16} = 6.89$, $P = 0.018$ and $F_{1,16} = 6.80$, $P = 0.019$). Link-weighted generality was also significantly decreased by insecticide in the maximum-effect phase (ANOVA, $F_{1,16} = 11.18$, $P = 0.006$) and increased by the herbicide, but decreased by the combination of the pesticides, in the recovery phase (ANOVA, $F_{1,16} = 4.32$, $P = 0.046$ and $F_{1,16} = 4.94$, $P = 0.040$, respectively).

We also found a significant correlation between the compositional log response ratio (LRR) and the interaction-strength LRR of all sampling days (Fig. 2).

Discussion

Effects of Single Pulse Disturbances. In this study, we assessed the value of ecological network analyses to better understand the differences between univariate and multivariate compositional descriptors of community composition and to identify ecological processes that may be responsible for long-term dissimilarity and late interactions between disturbances at the community level. Our study shows that changes in multivariate community composition were linked to changes in community biomass or diversity indexes after the disturbances' application (day 15, maximum-effect phase). After 50 d (recovery phase), all univariate descriptors of composition and function did not differ anymore from the control, indicating potential recovery. Yet, the analysis of multivariate composition showed that communities treated with a pulse application of insecticide or herbicide as a single disturbance were still significantly different from the control. Long-term compositional dissimilarities at the community level after pulse disturbance were reported in another study using aquatic communities (15) and have been observed in a wide range of ecosystems (2). Analyzing the food-web properties and interactions-strength dynamics, we found a coherent explanation for this apparent mismatch between univariate and multivariate descriptors of community composition, which has been reported extensively in the literature (4, 27, 28).

In the maximum-effect phase, topological properties were strongly influenced by the insecticide. Such properties are based on presence-absence interactions and thus heavily

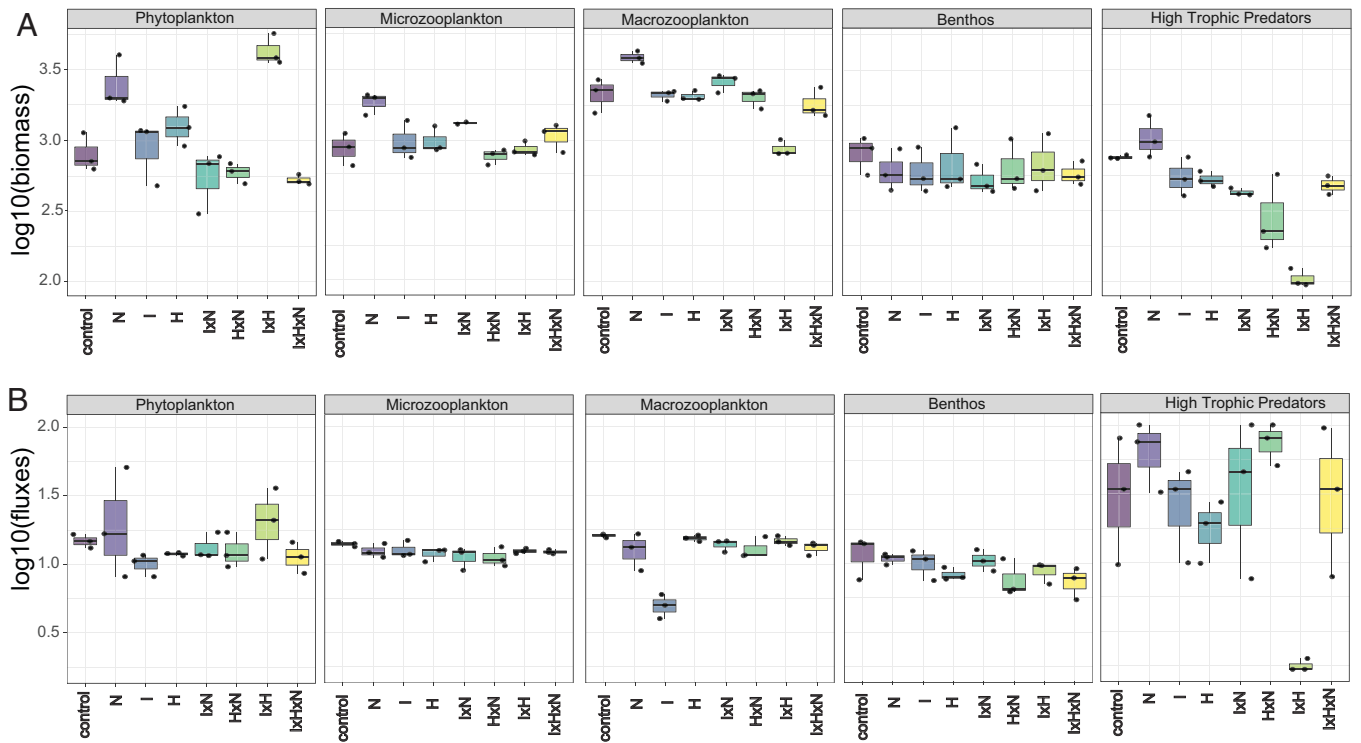


Fig. 4. Effects of the treatments on community biomass and interactions strength in the recovery phase. Box and whisker plots ($n = 3$, for all measures), where the center line indicates the median, and the bottom and top hinges of the box correspond to the 25th and 75th percentiles, respectively. Every replicate of each treatment is shown as an individual dot. (A) Log10-transformed biomass values for the different trophic groups across the treatments in the recovery phase. (B) Log10-transformed values of the sum of incoming and outgoing energy fluxes per trophic group across the treatments divided by the number of nodes/species contained in each trophic group. Such values represent the average interaction strength per each trophic group and how it varies in the different treatments. H, herbicide; I, insecticide; N, nutrients.

affected by the number of species (i.e., richness), which was indeed significantly reduced by the insecticide in the maximum-effect phase. Node-weighted properties (based on biomass) in the maximum-effect phase were significantly influenced by the herbicide. Consistently, nutrients enrichment and the herbicide were the only treatments modifying total community biomass in the same phase. In the recovery phase, when the effects of the pesticides were expected to be recovered, not a single property of the unweighted or of the node-weighted food webs was affected by the pesticides in isolation, and no univariate descriptor of community composition was significantly impacted.

Yet, looking at the link-weighted food-web properties, we found that connectance and generality were significantly modified by both pesticides applied as single disturbance in the recovery phase. An increase in link-weighted connectance suggests that several nodes/species have relatively high and similar energy flows (i.e., species-interactions strength), which increases link-weighted food-web complexity (23). Oppositely, a decrease in link-weighted connectance indicates an uneven distribution of energy flows, which may be clustered in a specific portion of the food web and disconnected from the whole network. In our model ecosystems, the herbicide increased link-weighted connectance, showing an even distribution of energy fluxes across the feeding guilds (Fig. 2B). This even distribution of interactions strength was also mirrored by the increase in link-weighted generality, which indicates an increased number of preys for each predator. Conversely, the insecticide caused a rewiring of the interactions strength that promoted the compartmentalization of energy fluxes (significant reduction in link-weighted connectance), reducing the outgoing energy fluxes from the macrozooplankton compartment, while expanding the outgoing fluxes

from basal species and benthic organisms (Fig. 2B). Subsequently, this increased the incoming flow to high-trophic predators feeding on benthic organisms (Fig. 3).

Overall, the analysis of single pulse disturbance on our experimental systems shows that, after pulse disturbance, communities may change in their univariate and multivariate composition, as well as in their functional parameters. However, biomass and diversity may be recovered, but the rewiring of interactions strength prevents communities to regain their concise composition. This was further sustained by the significant correlation between the relative changes in multivariate composition and the relative changes in the interactions' strength. Indeed, large compositional dissimilarities from the control were positively correlated with large differences in the interactions' strength, suggesting that changes in the intensity of species interactions may shape community composition. We propose that such rewiring of the interactions' strength is linked to the different sensitivities of the taxa to a specific disturbance. Our systems were populated by several species with different sensitivities to the disturbances applied. The initial decrease in univariate descriptors of composition was mainly caused by the decline of sensitive species (25, 29–31). Later, through recolonization (particularly of sensitive Ephemeroptera taxa, such as *Cloeon sp.* and *Caenidae*) or the development of resistance forms (e.g., ephippia and eggs in the case of Cladocera), the total number of species could be regained. Similarly, total biomass was recovered by compensation dynamics, where tolerant species increased their abundance at the expenses of declined sensitive species (32). Nonetheless, the predisturbance relative abundances of all taxa were not recovered, as indicated by the multivariate analysis of composition. We suggest that such community dissimilarity was driven by the tolerant species that persisted in the environment for the whole experimental time, causing the rewiring of the

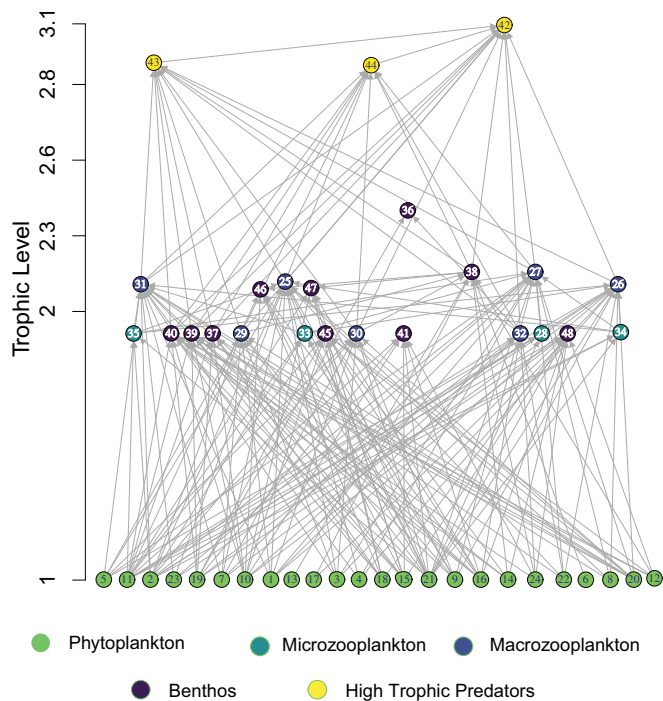


Fig. 5. The mesocosms food web before the start of the experiment: 1, *Ankyra* sp.; 2, *Monoraphidium* sp.; 3, *Oocystis* sp.; 4, *Pediastrum* sp.; 5, *Cosmarium* sp.; 6, *Staurastrum* sp.; 7, *Peridinium* sp.; 8, *Rhodomonas* sp.; 9, *Achanthes* sp.; 10, *Amphora* sp.; 11, *Cocconeis* sp.; 12, *Cymbella* sp.; 13, *Epithemia* sp.; 14, *Eunotia* sp.; 15, *Gomphonema* sp.; 16, *Navicula* sp.; 17, *Rhopalodia* sp.; 18, *Rhoicosphenia* sp.; 19, *Nitzschia* sp.; 20, *Synedra* sp.; 21, *Chroococcus* sp.; 22, *Microcystis* sp.; 23, *Oscillatoria* sp.; 24, *Spirulina* sp.; 25, *Daphnia pulex*; 26, *Simocephalus* sp.; 27, Cyclopidae; 28, Nauplii; 29, *Alonella* sp.; 30, *Alona* sp.; 31, *Ceriodaphnia* sp.; 32, Ostracoda; 33, *Keratella* sp.; 34, *Polyarthra* sp.; 35, *Ascomorpha* sp.; 36, *Erbodella* sp.; 37, Lumbriculidae; 38, Chironomidae; 39, Caenidae; 40, *Cleon* sp.; 41, Hydrobiidae; 42, *Notonecta* sp.; 43, Anisoptera; 44, Zygoptera; 45, *Dugesia* sp.; 46, Leptoceratidae; 47, Leptoceridae; 48, Lymnaea.

interactions strength in the food web highlighted by our analysis. Thus, compositional recovery was stonewalled by what could be called the “postdisturbance priority effect.” The priority effect (33) suggests that the order and timing of species immigration during community assembly may affect species abundances and cause historical contingency in the structure and function of the community. We build on this concept and suggest that, after a disturbance large enough to cause the decline of some populations within a community, a similar process drives the rewiring of interactions strength. The niche pre-emption and niche modification (33) carried out by the tolerant species that persisted in the community hampered the recovery of declined population through competitive exclusion and/or strong predation pressure (34). This was particularly evident in our systems, where the insecticide almost completely eradicated all Cladocera (e.g., *Daphnia* sp., *Ceriodaphnia*, *Simocephalus*, *Alona*, and *Alonella*) and Ephemeroptera (*Cleon* sp. and *Caenidae*) taxa in the maximum-effect phase (SI Appendix, Fig. S1). Yet, the Ephemeroptera taxa could recolonize the mesocosms successfully, whereas the Cladocera taxa regained an abundance level comparable to the control’s one only under eutrophic condition. Noneutrophic systems treated with the insecticide showed a dominance turnover in favor of the Cyclopoid copepods from the maximum-effect phase onward. Probably, in eutrophic systems, the zooplankton suffered less from competition, as the nutrients treatment assured higher energy provision after the insecticide pulse that led to an increased overall zooplankton biomass in the recovery phase (Fig. 4A). In turn, this decreased the phytoplankton biomass, owing to the increased

grazing pressure. Similarly, the herbicide treatment strongly reduced the abundance of the Chlorophyta after its application. This promoted a compensatory dynamic that increased Dinophytes abundance. Subsequently, Dinophytes competitively excluded some of the Chlorophyta, which never regained the pre-disturbance dominance (SI Appendix, Fig. S1).

We can conclude that interactions strength was rewired, which shifted network connectance and modified further single-population dynamics without modifying topological properties of the food web or univariate descriptors of community composition and function. Although these mechanisms have been long considered in theoretical ecology, in this work, such rewiring of species interactions is quantitatively assessed with empirical data and used to explain the reported delayed (or completely missing) compositional recovery of freshwater communities after pulse disturbance.

Effects of Nutrients Enrichment. Nutrients enrichment caused a significant shift in several unweighted and node-weighted properties throughout the experiment. Eutrophic systems, despite showing a simplification of the food web, which was reflected by the changes in the architecture of the network and by univariate descriptors, were characterized by a general increase in biomass (Fig. 4A) and interaction strength in the long term (Fig. 3). Eutrophication is known to increase the energy fluxes due to higher resources availability (35). Consequently, eutrophication increases the bottom-up energy supply, which may lead to the “paradox of enrichment” (36) and to a following decline in richness (37). However, in the context of this study, it should be noted that nutrients were applied before and throughout the experiment as a press perturbation; thus, significant effects for the whole experimental time were expected. The nutrients treatment was designed to look for possible interactions between pulse (pesticides) and press (eutrophication) disturbances, which were not identified in this study.

Multiple Disturbance Interactions. Pulse-disturbance interactions on multivariate community composition only appeared in the recovery phase in the herbicide–insecticide treatment under noneutrophic conditions. It is unlikely that this compositional change was driven by the sensitivity of the different taxa toward the disturbances, as in the recovery phase, the concentration of the pesticides was too low to be harmful for aquatic organisms (25, 38). The analysis of the link-weighted properties highlighted that in the recovery phase, the connectance and the generality of the food web were decreased by the mixture of the pesticides. Fig. 2B shows that the outgoing energy fluxes in this treatment were dominated (>80%) by the basal species, whereas the outgoing fluxes from higher trophic levels were drastically reduced, with no outgoing fluxes from the high-trophic predators. At the same time, Fig. 4B shows that the per capita average interaction strength (sum of ingoing and outgoing flows divided by the number of nodes/species) for top predators was extremely low compared to the other treatments, where high-trophic predators exerted strong interactions. Although both strong and weak interactions are essential in promoting the stability of ecological networks (39, 40), the disruption of strong trophic interactions has been previously shown to produce drastic cascading effects on food webs, which lead to changes in community structure (41). The loss of strong interactions from high-trophic predators, despite being well reflected by the changes in connectance and generality, also resulted in significant changes of the node-weighted properties. Node-weighted connectance was decreased by the pesticides mixture, driven by a reduction of high-trophic predators and

Table 1. List of unweighted and weighted food-web properties used, definitions, and relevant ecological information

Food web	Properties	Definition/relevance	Reference
Unweighted	Number of links	Number of trophic interactions in a food web. Represents the pathways along which matter and energy can flow.	68
	Link density	Average trophic interactions per species.	68
	Connectance	Proportion of actual interactions among possible ones. It is considered an estimator of community sensitivity to perturbations.	68
	Generality	Number of preys of a species normalized by the average number of preys across the food web.	69
	Vulnerability	Number of predators of a species normalized by the average number of predators across the food web.	69
	Number of basal and top species	Species without prey (basal) and without predators (top). Basal species define the shape at the base of the food web, while top ones may have indirect effects on other species via top-down control.	70
	Mean and maximum trophic levels	The trophic level is an indicator of the position a species occupies in a food web resuming the distance of each species to the source of matter and energy. It represents the energy-transfer efficiency from basal to top species.	71
	Omnivory	Proportion of species that feed at different trophic levels. It provides trophic flexibility to an ecosystem.	72
	Path length	It is the average distance, accounted by the number of interactions, between any pair of species. Food webs with low values might face a rapid propagation of disturbances.	73
	Clustering coefficient	It is a measure of grouping that reflects how likely is that two connected species are part of a larger, highly connected group. High values may buffer the spread of perturbations.	73
Node-weighted	Connectance, generality, vulnerability, mean trophic level	Species (nodes) are weighted by their biomass. For instance, mean trophic level of a food web corresponds to the average of species' trophic levels weighted by their biomass.	74
Link-weighted	Connectance, generality, vulnerability	Interactions (links) are proportional to the magnitude of energy fluxes. Properties were calculated by estimating the average effective number of preys and predators of each taxon weighted by their relative incoming and outgoing flows.	69

macrozooplankton biomass (Fig. 4A). Probably, the reduced grazing pressure derived from the pesticide-driven decrease in macrozooplankton biomass triggered an expansion at the base

at the food web, which was reflected as an increased phytoplankton biomass (Fig. 4A), resulting from decreased top-down control by the zooplankton and as an increase in diversity of

basal species (*SI Appendix, Table S3*). Despite the increased number of basal species, the mixture of pesticides reduced the total richness of the network in the recovery phase (*SI Appendix, Table S2*). Such reduction was then translated into significant changes in the topological properties of the food web (reduction in the number of links, link density, and generality; *SI Appendix, Table S3*). Particularly, the large changes in the relative abundances of macroinvertebrate composition (*SI Appendix, Fig. S1*) coupled with the reduced biomass of the zooplankton might have reduced the availability of preys for the high-trophic predators. High-order consumers are known to suffer disproportionately from instability at lower trophic levels (42). The changes at a lower trophic level thus may have led to a strong biomass reduction of the high-trophic predators.

That the loss of high-trophic predators may trigger rapid changes in community structure (41) and may lead to secondary extinctions (43) was already known. However, here, we show that the rewiring of the trophic interactions' strength, which led to a loss of strong interactions with high-trophic predators without causing their extinction, is sufficient to trigger a complete change in the food web (that is, topological as well as interactions strength).

Outlook and Future Directions. In this study, we investigated the differences between functional and compositional dynamics under different disturbance regimes. We show that functional and multivariate compositional responses to disturbance are substantially different. Importantly, we demonstrate that community biomass can be recovered, despite significant changes in community composition, supporting the idea that functional redundancy can ensure a similar level of functioning, even if species composition changes (1, 2). In line with other empirical studies (3, 4), our work suggests that under a changing environment are actually shifts in composition that allow maintaining biomass stable. Indeed, in field or semifield experiments (i.e., high richness), sensitivity-driven species turnover and changes in dominance after disturbance allow maintaining (or recovering) ecosystem functioning through species asynchrony (5, 6) (*SI Appendix, Fig. S1*). In this context, the eutrophication treatment deserves a particular mention. The press nutrients enrichment determined a reduction of species richness, but a general increase in biomass production. Nutrients' addition favors the growth of primary producers with high nutritional demands and fast uptake strategy. In turn, the fast-growing species cause an increase in competition for other resources (e.g., light or space), which determines the decline of the other slower-growing species. Thus, under eutrophic conditions, functioning levels can increase, despite changes in composition and a diversity decline (4, 7).

Recently, energy fluxes going from one trophic compartment to another have been proven to be a sensitive and meaningful way to measure ecosystem functioning in multitrophic systems (44–46) and have been used to quantify the effect of biodiversity loss on ecosystem functions (47). However, how different measurements of functional and compositional stability (48) relate to the temporal variation in fluxes has not yet been investigated. Further investigation in this direction may give rise to new hypotheses and shed light on the relationship between functional and compositional aspects of stability (49, 50). Regarding the frequent disturbance-driven compositional shift we found, our study suggests that the rewiring of the interactions' strength may be driving long-term compositional dissimilarity at the community level under both single and multiple disturbances. Interestingly, the only significant interaction between pulse disturbances on the community composition

appeared at a late stage and was associated with a complete change in the ecological network, which produced an expansion of the bottom of the food web and a decrease in high-order consumers. We identify interactions strength (or energy fluxes) rewiring as the driving mechanism of the restructuring in the food-web architecture. Consequently, it appears that changes in trophic structure and energy fluxes are key elements to understand—and potentially explain—the mechanisms driving the late appearance of interactions between disturbances at high levels of biological organization (14, 51, 52).

We do recognize, however, that our approach has some limitations. First, this study includes only negative trophic interactions. Nontrophic and positive interactions have been shown to play a role in determining the overall effects of interacting disturbances (19) and in shaping food webs (53). Additionally, although our work involves a relatively large number of species and links for experimental systems, it is still incomparable with real-world ecosystems, where food webs are larger and more complex. Future research that may succeed in including the analysis of nontrophic (competition or facilitation) and positive trophic interactions (mutualism) in food webs containing a larger number of high-trophic predators (i.e., vertebrates) has the potential to eviscerate the mechanisms driving communities' responses to disturbance at higher spatial resolution, as well as those causing the large compositional turnover reported at the global scale (54).

We are aware that the analysis of ecological networks poses great challenges, as the construction of food webs may be time- and resource-consuming. Moreover, resolving complex food webs at a high spatial scale is extremely laborious, if not impossible. Nonetheless, the application of food-web analyses to model ecosystems exposed to different types and gradients of disturbance may unveil mechanisms that explain ecological responses in natural ecosystems (55, 56). Communities and ecosystems are the primary target of management and policy makers (57, 58); thus, understanding the processes causing (unexpected) long-term interactions between disturbances is the first step toward increasing our predictive capacity of ecosystems response to multiple anthropogenic perturbations.

Materials and Methods

Experimental Design. The dataset used in this study was obtained from an outdoor mesocosm experiment performed between April and July of 2019 at the facilities of the Instituto Madrileño de Estudios Avanzados (IMDEA) Water Institute (Alcalá de Henares, Spain). A full factorial design was used with eight different treatments applied in a randomized fashion and three replicates per treatment. The treatments included: the insecticide chlorpyrifos (1 µg/L and absent), the herbicide diuron (18 µg/L and absent), nutrients (750 µg/L N and 75 µg/L P, not added), and their binary and tertiary interactions. The nutrients treatment started 1 mo before the application of the pesticides. Since then, N and P were applied twice a week for the whole duration of the experiment. The freshwater community tested in the experiment was composed of phytoplankton, zooplankton, and macroinvertebrates, which were sampled one time before and several times after the pesticide application. However, for the purpose of this study, we focus on days –5 (predisturbance condition), 15 (expected maximum effect), and 50 (expected recovery) relative to the pesticides' application. We expected recovery after 50 d based on previous mesocosm studies evaluating pulse exposure to these compounds (59, 60). Details on the experimental systems and the sampling techniques used in the experiment may be found in ref. 61.

Food-Web Construction. We used publications, personal observations, and the database built by Gray et al. (2015) (62), which represents the largest standardized collection of trophic links for freshwater organisms, to establish the trophic interactions among the species of the experimental mesocosms. For some phytoplankton and microzooplankton species, references on feeding preference

were not found, limiting the possibility to add these species to the network. In such cases, we aggregated the species for which feeding information was missing together with the closest taxonomically and/or size-wise species for which feeding information was available. A detailed list of the aggregations performed as well as on links' references may be found in *SI Appendix, Tables S1 and S2*. The resulting interaction list comprised 208 links and 48 trophic species (24 phytoplanktonic basal species, 12 zooplanktonic species, 9 benthonic macroinvertebrates, and 3 high-trophic predators; Fig. 5). A total of 72 networks were built (8 treatments including control \times 3 d \times 3 replicates), considering the biomass for each species. Information on biomass calculations can be found in *SI Appendix*.

Unweighted and Weighted Food-Web Properties. Two types of networks were defined to characterize the food webs for each mesocosm: qualitative or unweighted, formed by the presence or absence of interactions, and quantitative or weighted, where interactions' strength was also considered. For the first, we calculated the following unweighted food-web properties: number of links (L), link density (L/S, where S is the number of species), connectance (C), generality, vulnerability, number of basal and top species, mean trophic level, maximum trophic level, omnivory, path length, and clustering coefficient. We used the R package *multiweb* [Saravia et al., 2019 (63)] to obtain these properties. As for the weighted food webs, we used a bioenergetic approach to estimate interactions' strength, which enabled us to calculate weighted properties (23). Basically, this approach considers allometric scaling laws to quantify individual metabolic rates that are dependent on body mass and temperature, which, together with losses to predation and assimilation efficiencies, are used to quantify incoming fluxes (due to consumption) and outgoing fluxes (predation) for each species. Such an approach assumes the system's equilibrium or steady state, implying that the total amount of energy lost by a species, either by consumption or physiological processes, is exactly compensated by the metabolized energy it gains from consumption. This means that each species loss to predation and metabolism is balanced by its energetic gains, which are defined as incoming fluxes multiplied by assimilation efficiencies (64). For instance, to calculate energy flux from a food chain (i.e., species A is eaten by species B, which is consumed by species C), we start from the top predator (species C in the food chain) and assess how much energy this species needs. Given the assumption of the system's equilibrium, this energy needs to come out from the top predator's prey (species B). As such, it is assumed that the energy demand of species at a given trophic level must be met by the energy intake of that level. Due to ecological efficiencies (i.e., consumers cannot use all consumed energy to produce biomass; some is lost because of respiration and excretion), to fulfill its energy demands, every species needs to consume more energy from the next-lower trophic level. The energy consumed from this lower level is then treated as energy loss for the species at this level. This loss to consumption is then added to the energy demand of the prey species itself (species B) to represent the joint energy loss of this species that needs to be compensated by the next-lower level (species A), and so on. Therefore, top predators (species without predators) only have metabolic losses, while their prey, the herbivores, have both losses due to metabolism and consumption (64). The interaction-strength calculations in a food chain or food web begin from the top predator. In this way, the calculation of the interaction strength might be biased when there is a direct effect of the experimental treatments on the influx of energy. However, none of the treatments applied here (insecticide chlorpyrifos [1 μ g/L and absent], herbicide diuron [18 μ g/L and absent], and nutrients [750 μ g/L N and 75 μ g/L P, not added]) have been reported to directly affect the top predators of our food web (*Notonecta* sp., Anisoptera, and Zygoptera are the high-trophic predators; Fig. 5) (65,

66). Following Kortsch et al. (2021) (23), we calculated four node-weighted and three link-weighted food-web properties, where species' biomass and estimated energy fluxes were used, respectively. We calculated node-weighted connectance, generality, vulnerability, and mean trophic level, whereas as link-weighted descriptors of the food web, we calculated connectance, vulnerability, and generality. We used the R package *fluxweb* to estimate food-web fluxes (67). Table 1 provides an overview of the definition and ecological relevance of the food-web properties assessed in this study.

Statistical Analyses We analyzed the effects of single disturbances and their interactions on community composition using a PERMANOVA with 999 permutations (75), based on Bray-Curtis distances, obtained from log-transformed abundance data. PERMANOVA was performed by using the function "adonis2" from the R package *vegan* (76). To examine patterns in the whole community changes, we performed a nonmetric multidimensional scaling (NMDS) based on Bray-Curtis distances on abundance data for three sampling dates, representing the predisturbance condition (day -5 relative to the pesticides application), the moment of expected maximum effects (day 15 relative to the pesticides application), and the moment of expected recovery (day 50 relative to the pesticides application).

As univariate descriptors of community composition, we calculated species richness, Shannon's index, and community evenness using the R packages "BiodiversityR" (77) and "lawstat" (78). Also, we studied how the function of the community was affected by the treatments using total community biomass. Differences among indexes and biomass values caused by treatments were analyzed by means of a three-way ANOVA followed by a Tukey post hoc test in case of significant effects of the treatments. To test for significant effects of the treatments on all the different food-web properties calculated, we employed again three-way ANOVAs followed by a Tukey post hoc test. To check ANOVA's assumptions, we used the function "check_model" of the R package *performance* (79). If the assumptions were not met, we log- or sqrt-transformed the data to better fit the assumptions. To test for a correlation between the relative change in community composition and the relative change in interactions strength, we first calculated the LRR of the Bray-Curtis similarity of the community composition between each treatment and the controls: $LRR_{composition} = \ln\left(\frac{BC_t}{BC_c}\right)$. Then, we calculated the LRR of the interaction's strength between each treatment and the controls: $LRR_{interaction\ strength} = \ln\left(\frac{I_t}{I_c}\right)$. Finally, we calculated the nonparametric Spearman's rank correlation between the absolute values of compositional LRR and interaction-strength LRR. We used the absolute values of the LRRs, as we were interested in assessing whether changes in interactions strength are well reflected by changes in community multivariate composition. Thus, both negative and positive deviations from the control's interactions strength might be translated into compositional changes. All statistical analyses and food-web construction were conducted by using the R software (version 4.0.3).

Data Availability. Individual species-counts data have been deposited in the Zenodo repository (<https://doi.org/10.5281/ZENODO.6345884>) (80).

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