

Evidence for the persistence of food web structure after amphibian extirpation in a Neotropical stream

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Abstract. Species losses are predicted to simplify food web structure, and disease-driven amphibian declines in Central America offer an opportunity to test this prediction. Assessment of insect community composition, combined with gut content analyses, was used to generate periphyton–insect food webs for a Panamanian stream, both pre- and post-amphibian decline. We then used network analysis to assess the effects of amphibian declines on food web structure. Although 48% of consumer taxa, including many insect taxa, were lost between pre- and post-amphibian decline sampling dates, connectance declined by less than 3%. We then quantified the resilience of food web structure by calculating the number of expected cascading extirpations from the loss of tadpoles. This analysis showed the expected effects of species loss on connectance and linkage density to be more than 60% and 40%, respectively, than were actually observed. Instead, new trophic linkages in the post-decline food web reorganized the food web topology, changing the identity of “hub” taxa, and consequently reducing the effects of amphibian declines on many food web attributes. Resilience of food web attributes was driven by a combination of changes in consumer diets, particularly those of insect predators, as well as the appearance of generalist insect consumers, suggesting that food web structure is maintained by factors independent of the original trophic linkages.

Key words: *amphibian declines; Batrachochytrium dendrobatidis; chytrid fungus; connectance; food web structure; network analysis; periphyton–insect food webs; Rio Guabal, Panama; species loss.*

INTRODUCTION

Understanding effects of species losses on food web structure can help to address significant gaps in our knowledge of how declining biodiversity affects ecosystems (Thompson et al. 2012). Food webs depict who-eats-whom and can be used to characterize species interactions across multiple trophic levels. Previous food web research has predicted that, as highly connected species are extirpated, secondary extinctions (extinction cascades) will co-occur as remaining species lose resources (Dunne et al. 2002, Dunne and Williams 2009). More recently, models have examined effects of anthropogenic disturbances on food web structure, showing a simplification of food web structure with environmental degradation (Coll et al. 2008). Trophic linkages in these models are static, because the food webs studied either represent a snapshot in time (Thompson and Townsend 2005) or are aggregated over unspecified time scales (Martinez 1991). Such

models are implicitly “brittle” because they assume that trophic relationships are fixed and unable to compensate for species loss. However, in nature, trophic linkages are often dynamic, with consumers switching to different prey in response to the loss of a competitor or resource or changing abiotic conditions. Consequently, surviving species may mitigate the loss of a species on food web structure through adaptive foraging, such as diet expansion (Staniczenko et al. 2010). Food web structure may also be influenced through indirect effects, such as facilitation, which can result in unpredictable feedbacks, altering community composition and dynamics (Wootton 1994, Montoya et al. 2009). Trophic dynamics and indirect effects could mean that effects of species loss on food web structure cannot be adequately represented with static food web models, and that food web structure may not be coupled to, but rather independent of, the trophic interactions of which they are composed.

The lack of pre- and post-extirpation food web data is a major challenge to quantifying effects of biodiversity loss on food web structure. Analyzing snapshots of a food web over time, rather than analyzing an aggregated food web, can provide insight into how an ecological

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network responds to a disturbance (Cohen et al. 2009) and may aid in differentiating the roles of individual species within the community. The Tropical Amphibian Declines in Streams (TADS) project allowed us to analyze snapshots of a benthic stream food web before and after sudden catastrophic amphibian declines driven by the chytrid fungus *Batrachochytrium dendrobatidis* (Lips et al. 2006). This epizootic has been moving from Costa Rica through Panama, creating a natural experiment, allowing for pre- and post-decline comparisons (Whiles et al. 2006, 2013). Previous TADS studies illustrated how the extirpation of larval amphibians (tadpoles) affected ecosystem properties, showing increased algal standing stock (Connelly et al. 2008) and decreased production of predator and shredder macroinvertebrates in Rio Guabal, a Panamanian highland stream (Colón-Gaud et al. 2010b). Tadpoles also consumed algae (Ranvestel et al. 2004, Barnum et al. 2013) and probably were connected to the benthic food web through multiple trophic linkages. Consequently, tadpole extirpation may have affected food web structure and led to cascading extirpations of other species.

In this paper, we quantified differences in the structure of periphyton–insect stream food webs, with and without amphibians, in the Rio Guabal. We predicted that the structure of food webs without amphibians would be simplified (e.g., reduced complexity) compared to food webs with amphibians. Second, we determine the effects of extinctions on a static food web through computer simulations. We reasoned that if the attributes of the post-decline food webs were similar to simulated food webs, then static food webs could be effective tools for assessing effects of species loss. However, if the attributes of the post-decline food web were similar to the pre-decline food web, then indirect effects might have a significant role in structuring food web topology.

METHODS

Study system

Rio Guabal is a headwater stream at ~750 m above sea level in the Parque Nacional G.D. Omar Torrijos Herrera, El Copé, Coclé, Panama (8°40' N, 80°35' W). The stream is characterized by distinct pool-run/riffle sequences with a gravel and boulder substrate. Canopy cover is >80%, with occasional tree fall gaps (Connelly et al. 2008). Discharge during sampling in 2004 and 2009 was almost identical at 58 L/s and 60 L/s, respectively, and the stream never dried between the two sampling events (Connelly et al. 2014). The stream had 23 species of stream-dwelling tadpoles occurring in all stream habitats, including riffles, runs, pools, detrital leaf packs, and marginal pools (Lips et al. 2003). The most abundant tadpoles in riffle habitats were *Atelopus varius*; *Lithobates warszewitschii*, *Hyloscirtus colymba*, and *Hyloscirtus palmeri* were abundant in pool habitats (Ranvestel et al. 2004). Amphibian declines in this

region began in September 2004 and continued through January 2005 (Lips et al. 2006). Two species of fish (*Brachyraphis roswithae* and *Trichomycterus striatus*), along with shrimp (*Macrobrachium* spp.) and crabs (*Pseudothelphusa* sp.) also occurred within the stream, but were not included in the food web analysis. The most abundant fish, *B. roswithae*, are surface feeders (Ranvestel et al. 2004) and *T. striatus* were extremely uncommon, with only one individual observed on 14 consecutive days of sampling a 500-m reach in April 2009. Crabs and shrimps were also excluded from the food web because of their low abundance in the riffles and pools that were sampled (Ranvestel et al. 2004, Connelly et al. 2008).

Food web construction

Rio Guabal's benthic community was assessed over a 500-m reach during the dry season, three times pre-decline (4 February, 5 March, and 7 April 2004) and three times post-decline (18 February, 23 March, and 7 April 2009). Five years separated sampling events to allow time for populations to respond to amphibian declines. Tadpoles were collected from the stream in 2004 following methods described in Colón-Gaud et al. (2010b). For permitting reasons, the tadpoles of *A. varius* were collected from a stream a few kilometers to the east, in the Altos del Piedra, Panama, in February 2004. The Altos del Piedra was of similar size and elevation as our focal stream, and insect and diatom assemblages are similar across sites at this elevation (Colón-Gaud et al. 2010b, Rantala et al. 2015). Invertebrates were sampled each month using six stove-pipe benthic core samples (314-cm² sampling area) from pool habitats and eight Surber samples (930-cm² sampling area) from riffle/run habitats. Invertebrates were identified to genus (except Chironomidae) and were measured to estimate biomass using methods described in Colón-Gaud et al. (2010b); see Appendix A. From 7 to 22 April 2009, additional, haphazard sampling for invertebrates using a D-net was done to increase the sample size for gut content analyses of rarer taxa. The diatom and algae community on natural substrata were sampled from five riffles and pools on the same days and from the same reach as the macroinvertebrate community, using a benthic sampler (modified after Loeb 1981) during base flow. Diatom community composition was assessed using the methods in Connelly et al. (2008), with a minimum of 600 diatom frustules identified to genus from each sample. Diatom densities for each genus are reported in Appendix B.

Food web linkages were identified through gut content analyses, using individuals collected for biomass estimates during the latter part of the dry season in March and April 2004 and April 2009. These months were selected due to the presence of the largest dragonfly instars, which emerge during the transition between the dry and wet season (Pritchard 1996). The number of prey items for these predators increases with body size

(Woodward and Hildrew 2002), maximizing the number of predator–prey linkages that we could identify. For the analysis of gut contents and construction of food webs, insect taxa with a biomass > 2 mg ash-free dry mass (AFDM) per square meter per month were selected, whereas taxa with a smaller biomass generally had less than one individual collected each month and were excluded from the analysis. This criteria excludes rare and small taxa (e.g., riffle beetle larva and uncommon mayfly genera), but not taxa that were rare but big, such as the odonate *Argia*. The riffle beetle and mayfly genera that were excluded had sister genera that were included, making the exclusion of these rarer taxa unlikely to change our main results.

Guts of algal-grazing tadpoles and non-predator macroinvertebrates were removed and suspended in water, filtered onto a nitrocellulose membrane, slide-mounted, and then sealed with a coverslip and nail polish. The gut contents were then examined for diatoms and animal fragments through oil immersion brightfield optics at 1000 \times on an Olympus CH30. For each gut, a maximum of 300 diatoms were identified to genus in up to 10 measured transects. Plant material and filamentous algal cells were noted and included in the food web. Gut contents of macroinvertebrate predators were removed and the head capsules of prey items were used to identify prey to genus. Guts were then prepared using the same technique as tadpoles and non-predator macroinvertebrates. The filter was scanned at 100 \times for prey fragments such as cerci and tarsi and then examined at 1000 \times for additional prey items and diatoms until a maximum of 300 diatoms were identified to genus in up to 10 measured transects. The number of individuals sampled per taxon depended on the availability of specimens and ranged from 4 to 21 individuals. All gut content analyses were performed in 2010–2011, with the same person identifying all diatoms to ensure consistent identification of diatom genera (diatom frustules are made from silica and do not break down in seven years). Furthermore, gut content analyses were staggered, with only five individuals per genus from each year being prepared and analyzed at any one time, ensuring consistent identification of diatoms for both food webs through time. Rarefaction curves for each taxon were created to assess sampling effort. Additional linkages that would be discovered with further sampling were estimated using the Chao2 species estimator in EstimateS (Colwell et al. 2012; see Appendix C).

Four food webs of the benthic community were constructed for pools pre-amphibian decline (2004); riffles pre-amphibian decline (2004); pools post-amphibian decline (2009); and riffles post-amphibian decline (2009). Separate food webs with nodes (“species”) and linkages (trophic interactions) were created for riffles (faster water flow/shallower depth) and pools (slower water flow/deeper depth) because these two habitats contained distinct tadpole assemblages. Nodes within the food web were identified to genus because this was

the lowest taxonomic level that we could use while keeping taxa in functionally similar groups across time. Trophic interactions between species were included when a prey item was identified at least once in the gut of the consumer.

Network analyses

For each of the four food webs, we examined characteristics of the whole network and individual nodes. A node’s *degree* is the number of incoming and outgoing linkages, and the frequency of occurrence of degrees within the network defines the *degree distribution*. *Betweenness centrality* is a measure of central position in the food web, which, for each species *i*, is defined as the fraction of species pairs *j* and *k*, such that species *i* falls on the shortest path from *j* to *k* (Estrada 2007, Jordán et al. 2007). Species with a high betweenness centrality are important because they mediate many indirect interactions between species (Estrada 2007) and are topological “hubs” in a food web (Lai et al. 2012). For the whole food web network, we examined 15 coarse-grained attributes that, based on a search of the literature, are predicted to change as a consequence of species loss (Table 1). These coarse-grained attributes included summaries of the degree distribution, including linkage density, connectance, skewness, and variance of the degree distribution. Although linkage density and connectance are commonly measured food web characteristics, skewness and variance of the degree distribution are less commonly calculated. We included them in our analysis because they summarize the tendency of the network to be structured by only a few key taxa vs. diffuse interactions distributed over many taxa. Particularly, a right-skewed degree distribution indicates relatively few taxa with many linkages, while a left-skewed degree distribution indicates a large number of taxa with many linkages. The variance of the degree distribution is important for showing the dispersion around the mean. Other coarse-grained food web attributes were size of the network (number of species); average path length; maximum trophic level; generality; vulnerability; and fraction of species in the categories basal taxa; herbivores; intermediate consumers; top predators; omnivores; and cannibals. Food web attributes, including betweenness centrality, were calculated in R version 2.15.2 (R Core Team 2013) using the igraph (Csárdi and Nepusz 2006), e1071 (Meyer et al. 2014), our own R scripts, and Foodweb packages (*available online*).⁸

Calculated cascading extirpations

We calculated the expected number of cascading extirpations using two methods. First (Sim 1), we started with the adjacency matrix depicting the food webs for both pools and riffles for 2004, and removed tadpole and

⁸ <http://cran.r-project.org/web/packages/foodweb/foodweb.pdf>

TABLE 1. Food web attributes used to characterize food web structure and that were predicted to change (downward arrows, decrease; upward arrow, increase) following tadpole declines in Rio Guabal, Panama, based on a review of the literature.

Term	Attribute	Description	Prediction	Reference
S †	species richness	number of trophic species	↓	2
L/S	linkage density	number of linkages per species	↓	2
C	connectance	fraction of realized links (L/S^2)	↓	2
Skew‡	skewness	asymmetry of the degree distribution	←	2
Var‡	variance	variance of the degree distribution	NP	NP
Path	average path length	average shortest path length between all species pairs	↓	1
MaxTL	maximum trophic level	maximum trophic level of the top predator	↓	3
Gen	generality	standard deviation for number of prey per species	↑	1
Vul	vulnerability	standard deviation for number of predators per species	↓	1
% Bas	fraction of basal taxa	fraction of taxa with no prey	↑	1
% Herb	fraction of herbivores	fraction of taxa that feed on basal taxa	↑	2
% Int	fraction of intermediate consumers	fraction of consumers with predators and prey	↑	2
% Top	fraction of top predators	fraction of consumers with prey, but no predators	↓	2, 4
% Omn	fraction of omnivores	fraction of species that feed at more than one trophic level	↓	1
% Cann	fraction of cannibalism	fraction of species that feed on their own species	↓	1

Notes: The prediction for skewness is that the degree distribution will become more left-skewed (left-pointing arrow) following a species loss. Variance is not predicted (NP) to change following species loss.

† For richness, S , species with the same prey and predators are usually lumped into trophic groups. However, we needed to account for changes in diet in response to species loss and wanted to maintain the criteria for S to be consistent across time. Therefore, we used the number of genera (except for Chironomidae which were classified as non-Tanytopodinae and Tanytopodinae) for S because genus was the lowest taxonomic level we could use while keeping taxa in functionally similar groups. Reference are: 1, Coll et al. (2008); 2, Dunne et al. (2002); 3, McHugh et al. (2010); 4, Odum (1985).

‡ Attributes uncommon in food web literature.

macroinvertebrate taxa with a biomass < 2.0 mg AFDM per square meter per month in 2009. Next, any taxa that were no longer connected to the food web were also removed. The second calculation (Sim 2) started with the adjacency matrix for 2009 and then only retained species present in 2004, thus excluding species that were lost from the community between 2004 and 2009 as well as species that arrived after amphibian declines, to test if observed differences in food web structure from 2004 to 2009 were the result of new species or newly formed connections among the original species. Following these simulated extinctions, the 15 network attributes and betweenness centrality were recalculated for the simulated food webs. These simulated extinctions provided a numerical prediction of the change in food web structure, given the “brittleness” assumption that food web structure depends on its constituent species and does not adapt to perturbations.

The effect of extirpation on each food web attribute was calculated by comparing the attributes from the constructed pre-decline and post-decline food webs to the food webs that simulated primary and secondary extinctions ($z = (\text{post-decline} - \text{Sim 1})/(\text{pre-decline} - \text{Sim 1})$) For any given food web attribute, $z = 0$ indicates that the post-decline food web is identical to that predicted by simulations and supports the hypothesis that static food webs can be effective tools for assessing effects of species loss. Values of $z < 0$ indicate that a food web attribute has changed more than the simulated loss would predict. Cases where $0 < z < 1$ indicate that the post-decline food web is intermediate between simulated and pre-decline and that the food web exhibits some degree of structural resilience to species loss. Of these, attributes for which $z > 0.5$ are more similar to

the pre-decline food web, whereas those for which $z < 0.5$ are more similar to the simulated species loss. For example, if connectance was 0.17 pre-decline and 0.14 post-decline, and simulation 1 predicted a connectance of 0.13, then z would be 0.25, indicating some food web resilience to species loss.

The food webs that excluded extinct species as well as species that arrived after amphibian declines (Sim 2) were then compared ($z = (\text{Sim 2} - \text{Sim 1})/(\text{pre-decline} - \text{Sim 1})$) to test if observed differences in food web structure from 2004 to 2009 were the result of new species or newly formed connections among the original species. For any given food web attribute, $z = 1$ indicates that the Sim 2 food web is more similar to the Sim 1 food web, suggesting that resilience in food web structure is driven by newly formed connections among original species. Values of $0 < z < 1$ indicate that the Sim 2 food web attribute is intermediate between Sim 1 and pre-decline. Attributes for which $z > 0.5$ are more similar to the Sim 1 food web, suggesting that the resilience in food web structure post-decline is driven by the arrival of new species into the community. For example, if connectance was 0.17 pre-decline and 0.16 in Sim 2, and Sim 1 predicted a connectance of 0.14, then z would be 0.67, indicating that resilience in food web structure was driven by newly formed connections among the original species.

RESULTS

Empirical network analysis

The total number of taxa in the food web (including tadpoles, macroinvertebrates, and diatoms) declined from 60 to 44 (25%) in pools and from 65 to 55 (15%) in riffles from February–April 2004 to February–April

2009 (Fig. 1). In pool habitats, nine of the 17 macroinvertebrate taxa present in 2004 were present in 2009, while there was one new macroinvertebrate taxon present in 2009 (Appendix A). Riffle habitats experienced similar declines in macroinvertebrate taxa, with 15 of the 28 macroinvertebrate taxa present in 2004 remaining in 2009, while there were five new macroinvertebrate taxa in 2009 (Appendix A).

In total, 891 tadpole and macroinvertebrate guts were analyzed and 1793 linkages were identified from the four food webs. Gut content analysis yielded 18 128 observations for pools in 2004, 17 187 observations for pools in 2009, 54 308 observations for riffles in 2004, and 38 214 observations for riffles in 2009. The means from the species estimator curves indicated that 85–90% of all trophic linkages in the each of the four food webs were identified (Appendix C).

In pool habitats, 303 of the 412 linkages (73%) in 2004 were absent in 2009, whereas 98 of the 207 linkages (45%) in 2009 were absent in 2004 (Fig. 1a, b). Four predator taxa accounted for 57 of 98 new linkages (58%), with 51 of the 57 linkages occurring between predators and diatoms. The number of diatom valves and algal cells in the guts of these four predators increased from 141 ± 47 per gut (mean \pm SE) in 2004 to 429 ± 75 per gut in 2009 ($P = 0.001$) (Appendix D). Nineteen (19%) of the new linkages were associated with *Macrelmis*, a taxon absent from the pre-decline food web. The remaining 22 (22%) linkages were between herbivores and diatoms. Connectance declined by 7.1%, from 0.114 in 2004 to 0.107 in 2009, whereas linkage density declined by 30.6%, from 6.86 in 2004 to 4.76 in 2009 (Table 2).

In riffle habitats, 390 of the 658 linkages (59%) present in 2004 were absent in 2009, whereas 222 of the 489 linkages (47%) in 2009 were absent in 2004 (Fig. 1c, d). The five insect taxa that were only found post-decline accounted for 140 (63%) of these 222 new linkages, with 130 linkages occurring between diatoms and insects. These five new insect taxa were connected to a significantly larger number of species than surviving consumers from the pre-decline food web (Wilcoxon rank sum Test, $W = 20.5$, $P = 0.002$). Nineteen (8%) of the new linkages were extant insects consuming other insects. Eighteen (8%) of the remaining 63 linkages were between diatoms and predators, with 13 of these linkages occurring between odonates and diatoms. The odonates, *Philogenia* and *Heteragrion*, also had increased densities of diatoms and filamentous algae (*Audouinella chantransia*) in their guts post-amphibian decline (from 110 ± 67 per gut in 2004 to 2365 ± 756 per gut (mean \pm SE) in 2009, $P = 0.02$; and 50 ± 30 per gut in 2004 to 443 ± 79 per gut in 2009, $P = 0.001$, respectively) (Appendix D). The remaining 45 (20%) linkages were between herbivores and diatoms. Connectance increased by 5.8%, from 0.153 in 2004 to 0.162 in 2009, whereas linkage density declined by 11.9% from 10.1 in 2004 to 8.89 in 2009 (Table 2). In post-decline

food webs from riffles and pools, fewer taxa had lots of linkages as the degree distributions became more left-skewed.

The identity of those taxa that were central to the food web also changed from 2004 to 2009, as taxa with the highest betweenness centrality indices changed (Table 3). In 2004, the tadpoles (*Lithobates* and *Hyloscirtus* in pools and *Atelopus* in riffles) had the highest centrality values. In 2009, seven of the 10 taxa in pools and eight of the 10 taxa in riffles with the highest centrality values were not ranked in 2004.

Calculated extirpations

The z scores for several post-decline food web attributes that are associated with food web complexity (e.g., connectance, maximum trophic level, and omnivory), were either close to 1 or exceeded 1, indicating that the attributes from post-decline food webs were more similar to pre-decline attributes than expected (Fig. 2). The second simulation tested whether new species or newly formed connections among the original species contributed more to maintaining food web structure. In riffles, the z score was near 0, indicating that post-decline food web structure in this community was driven by the presence of new species. In pools, the z score was near 1, indicating that post-decline food web structure was driven by newly formed connections among original species (Fig. 2).

DISCUSSION

Our findings show smaller effects of species loss on food web structure than predicted through species deletions, challenging predictions of species loss from food webs that assume fixed trophic linkages. Specifically, in our study stream, food web structure persisted despite a 48% decline in consumer diversity (macroinvertebrates and tadpoles) from 2004 to 2009. The resilience of food web structure was driven primarily through two pathways: the appearance of new generalist consumers in riffles and diet expansion by predators in pools. Each pathway in each habitat accounted for ~60% of the new linkages. Although the attributes that describe food web topology changed little from pre- to post-decline, many new linkages and genera massively reconfigured the food web, changing the identity of “hub” taxa in the periphyton–insect food web. Consequently, in the post-decline food web, many attributes associated with food web complexity remained similar to those of pre-decline food webs. The resilience of food web structure to species loss suggests that factors independent of the original trophic linkages, such as indirect effects and diet expansion, may have played a significant role in maintaining food web structure.

Food web persistence is unlikely to be the result of intra- or interannual variation. Some coarse-grained attributes, such as connectance, can exhibit intra-annual variability, but this variability is driven by the availability of resources (Woodward et al. 2005). In our study

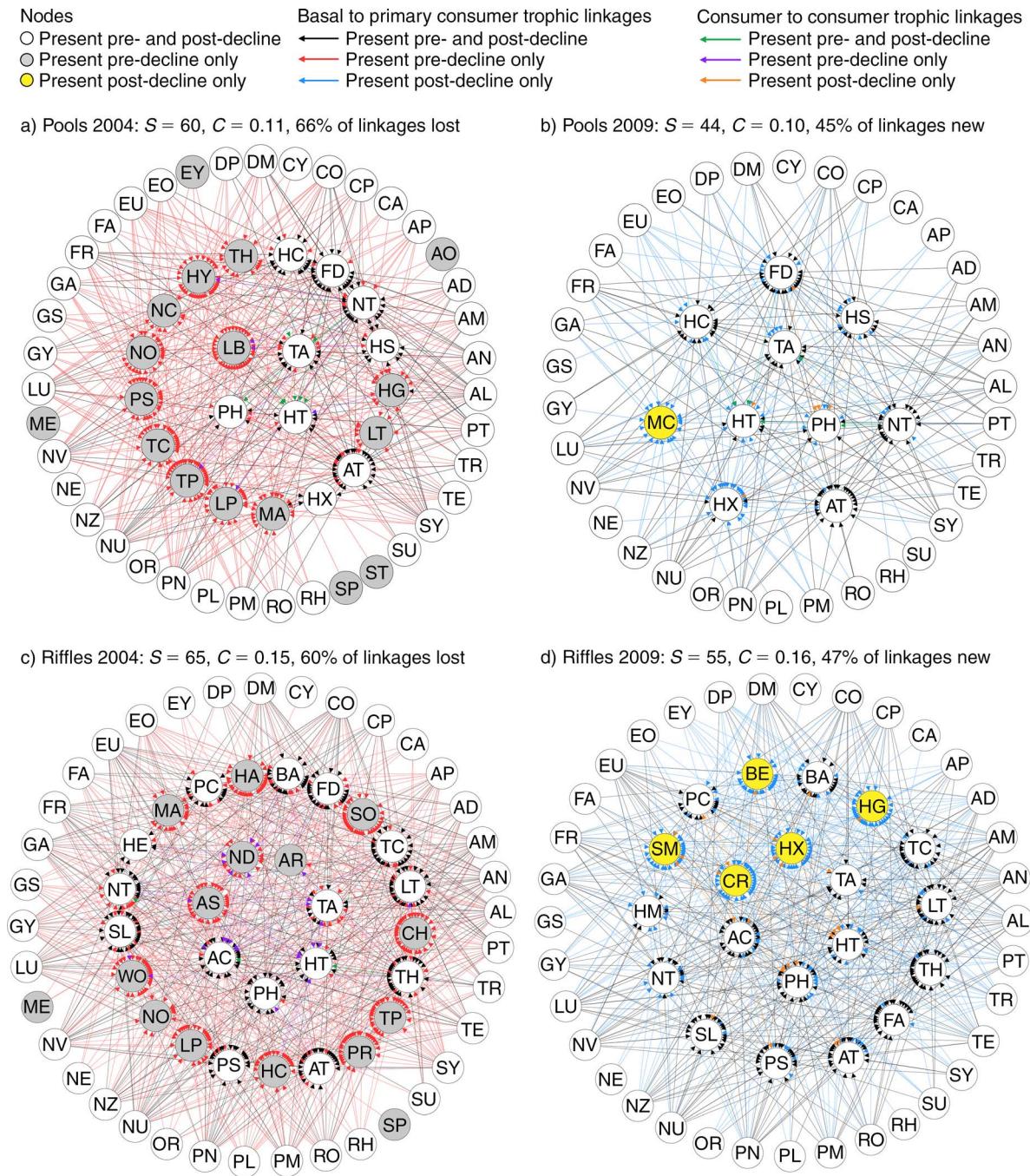


FIG. 1. A schematic diagram of food webs (a and c) pre- (2004) and (b and d) post- (2009) amphibian decline from pools (a and b) and riffles (c and d), with lines representing trophic linkages and circles representing species. Basal taxa (primary producers and plant detritus) are located on the outer circle, primary consumers (tadpoles and insect grazers) on the middle circle, and intermediate consumers and top predators on the innermost circle. Values are given for species richness (S) and connectance (C). Taxa abbreviations are: AC, *Anacroneria*; AD, *Adlafia*; AL, *Audouinella*; AM, *Achnanthydium*; AN, *Achnanthes*; AR, *Argia*; AO, *Amphora*; AP, *Amphipleura*; AR, *Argia*; AS, *Atelopus*; AT, *Anchytarsus*; BA, *Baetodes*; BE, *Baetis*; CA, *Caloneis*; CH, *Chimarra*; CO, *Cocconeis*; CP, *Chaempinnularia*; CR, *Cora*; CY, *Cyclotella*; DM, *Diadopsis*; DP, *Diploneis*; EO, *Eolimna*; EU, *Eunotia*; EY, *Encyonema*; FA, *Fallacia*; FD, *Farrodes*; FR, *Frustulia*; GA, *Gomphonema*; GS, *Gomphosenia*; GY, *Gyrosigma*; HA, *Haplohyphes*; HC, *Hexacyllopus*; HE, *Heterelmis*; HG, *Hagenulopsis*; HT, *Heteragrion*; HX, *Hexatoma*; HY, *Hyloscirtus*; LB, *Lithobates*; LP, *Leptohyphes*; LT, *Leptonema*; LU, *Luticola*; MA, *Macronema*; MC, *Macrelmis*; ME, *Melosira*; NC, *Nectopsyche*; ND, *Neurocordulia*; NE, *Neidium*; NO, *Neolmis*; NT, *Non-tanypodinae*; NU, *Nupela*; NV, *Navicula*; NZ, *Nitzschia*; OR, *Orthosiera*; PC, *Phanocerus*; PH, *Philogenia*; PL, *Placoneis*; PM, *Planothidium*; PN, *Pinnularia*; PR, *Petrophila*; PS, *Psephenus*; PT, plant; RH, *Rhoicosphenia*; RO, *Rhopalodia*; SL, *Simulium*; SM, *Smicridea*; SO, *Stenonema*; SP, *Stephanodiscus*; ST, *Stenoterobia*; SU, *Surirella*; SY, *Synedra*; TA, *Tanypodinae*; TC, *Tricorythodes*; TE, *Terpsinoe*; TH, *Thraulodes*; TP, *Tipula*; TR, *Tryblionella*; WO, *Wormaldia*.

TABLE 2. Topological attributes for pre-amphibian decline (2004), post- amphibian decline (2009), and the simulated removal (Sim1 and Sim2) of tadpoles and macroinvertebrates from pool and riffle food webs.

Term	Pools				Riffles			
	2004	2009	Sim1	Sim2	2004	2009	Sim1	Sim2
<i>S</i>	60	44	41	42	65	55	48	49
<i>C</i>	0.11	0.10	0.08	0.10	0.15	0.16	0.15	0.14
<i>L/S</i>	6.8	4.7	3.4	4.47	10.1	8.9	7.3	7.1
Skew	0.63	1.08	2.03	1.25	-0.61	0.088	0.71	-0.24
Var	77	60	51	61	81	74	73	71
Path	1.10	1.17	1.23	1.18	1.16	1.13	1.10	1.10
MaxTL	2.47	2.29	2.26	2.29	2.77	2.30	2.30	2.30
GenSD	1.57	1.92	2.26	1.99	1.25	1.38	1.60	1.58
VulSD	0.98	0.78	0.78	0.72	1.01	0.86	0.82	0.80
% Basal	0.65	0.77	0.78	0.79	0.57	0.64	0.69	0.69
% Herb	0.23	0.13	0.14	0.09	0.29	0.20	0.21	0.18
% Int	0.33	0.11	0.15	0.17	0.42	0.33	0.27	0.29
% Top	0.016	0.044	0.073	0.048	0.015	0.033	0.041	0.020
% Omn	0.11	0.12	0.06	0.07	0.17	0.16	0.15	0.12
% Cann	0.067	0.00	0.00	0.00	0.031	0.00	0.041	0.00

Notes: All attributes are unitless measures. Sim1 assumes that trophic linkages are static by using the 2004 food web, but with taxa absent in 2009 removed. Sim2 tests whether food web resilience is driven by new species or the formation of new linkages by using the 2009 food web and removing taxa present only in 2009. Food web terms are defined in Table 1.

stream, macroinvertebrates are multivoltine (with the exception of odonates), with overlapping generations, resulting in a range of size classes present in the stream year round (Colón-Gaud et al. 2010b) and suggesting that resource availability for insect predators is not temporally variable. However, previous TADS studies showed decreased benthic macroinvertebrate community diversity in the six months following amphibian extirpations (Colón-Gaud et al. 2010a, b). Macroinvertebrate diversity had declined by 48% in Rio Guabal four years post-amphibian extirpation (Appendix A), similar to the 42% decline in Rio Maria, a highland

stream ~30 km to the east of Rio Guabal, six years post-amphibian extirpation (Rantala et al. 2015). Populations of diatom genera also fluctuate little between the wet and dry season and only underwent major changes in community composition after amphibian declines (Connelly et al. 2008), suggesting that resource availability for grazing macroinvertebrates is not temporally variable.

Interannual variations in environmental conditions can also affect stream communities, but we saw no evidence for any changes except those associated with the loss of amphibians. For example, sedimentation can

TABLE 3. Betweenness centrality (Centrality) indices for taxa, including macroinvertebrates (M), diatoms (D), and tadpoles (T), with the 10 highest values for pre-decline (2004) and post-decline (2009) from pools and riffles.

Stream habitat	Pre-decline (2004)		Post-decline (2009)	
	Taxon	Centrality	Taxon	Centrality
Pools	<i>Lithobates</i> (T)	316.9	<i>Farrodes</i> (M)	224.9
	<i>Hyloscirtus</i> (T)	158.1	<i>Heterelmis</i> (M)	101.6
	<i>Tipula</i> (M)	131.7	<i>Anchytarsus</i> (M)	97.1
	<i>Anchytarsus</i> (M)	101.4	<i>Macrelmis</i> (M)	82.2
	non-Tanyptodinae (M)	92.6	<i>Hexatoma</i> (M)	78.9
	<i>Nupela</i> (D)	61.7	non-Tanyptodinae (M)	57.9
	<i>Psephenus</i> (M)	60.6	<i>Hexacylloepus</i> (M)	52.2
	<i>Navicula</i> (D)	57.3	<i>Heteragrion</i> (M)	34.8
	<i>Neelmis</i> (M)	56.9	Tanyptodinae (M)	26.0
	<i>Tricorythodes</i> (M)	53.8	<i>Philogenia</i> (M)	11.3
Riffles	<i>Atelopus</i> (T)	124.3	<i>Anacraoneuria</i> (M)	129.3
	<i>Simulium</i> (M)	118.6	<i>Cora</i> (M)	112.5
	<i>Thraulodes</i> (M)	91.8	<i>Philogenia</i> (M)	85.3
	non-Tanyptodinae (M)	88.3	<i>Hexatoma</i> (M)	58.5
	<i>Chimarra</i> (M)	68.9	<i>Thraulodes</i> (M)	58.1
	<i>Stenonema</i> (M)	64.5	<i>Anchytarsus</i> (M)	57.9
	Filamentous algae (D)	64.0	<i>Hagenulopsis</i> (M)	52.6
	<i>Leptonema</i> (M)	59.9	<i>Smicridea</i> (M)	45.2
	<i>Anchytarsus</i> (M)	54.0	<i>Leptonema</i> (M)	41.2
	<i>Wormaldia</i> (M)	50.5	<i>Baetis</i> (M)	37.5

Note: Betweenness centrality is a measure of a species importance to the food web's topology, with higher values indicating a central, or "hub," role for those taxa in the food web.

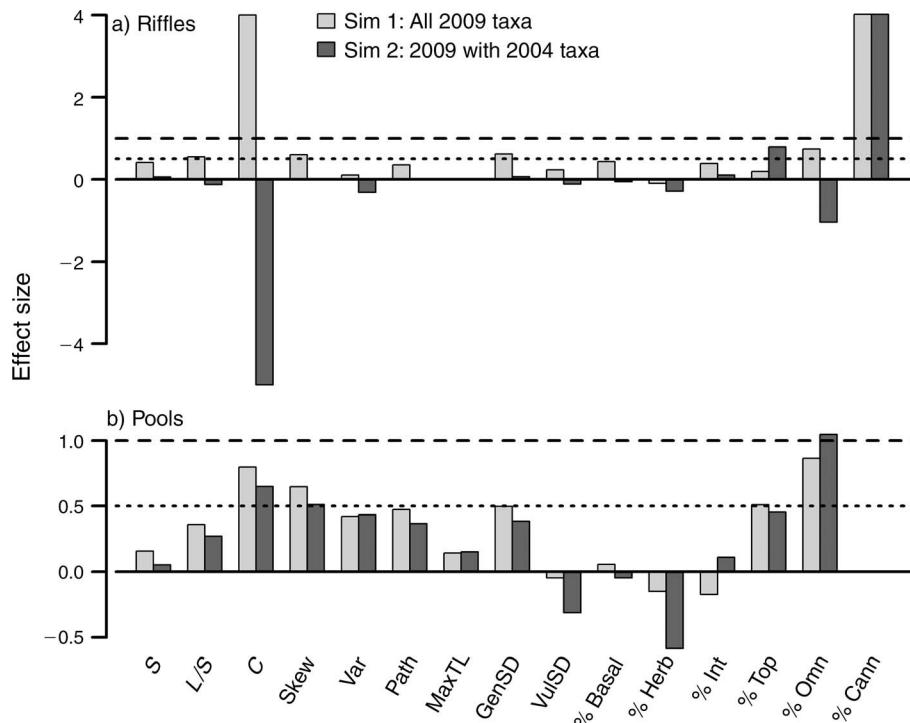


FIG. 2. The effect of amphibian declines on food web attributes for (a) riffles and (b) pools. Any z score above 1 (dashed line) signifies that the attribute from the pre-decline food web is intermediate to the post-decline and simulated food web. A number between 0 (solid line) and 0.5 (dotted line) signifies that the attribute from the post-decline food web is more similar to the simulated food web, and a number between 0.5 and 1 signifies the attribute from the post-decline food web is more similar to the pre-decline food web. Values <0 indicate that the attribute changed more than the simulation predicted. Connectance (C), linkage density (L/S), and maximum trophic level ($MaxTL$) are important indicators of food web complexity. Sim1 (light bars) reflects the simulated removal of tadpoles and macroinvertebrates from the pre-decline food web and is compared to the intact 2009 food web. Sim2 (dark bars) reflects the 2009 food web with only 2004 extant taxa (excludes taxa that were lost from the community between 2004 and 2009 and new species in the 2009 community) and is compared to the 2004 food web to determine if the resilience of food web structure was driven by the arrival of new species or newly formed linkages among the original species. Abbreviations for food web attributes are defined in Table 1.

reduce macroinvertebrate populations (Connolly and Pearson 2007), but sediment accrual in Rio Guabal was attributed to amphibian declines, even four years post-decline (Connelly et al. 2014). Anthropogenic causes of sedimentation, such as agricultural runoff or silt from road crossings, were not factors, because our study stream drained an undisturbed mountain forest catchment. Furthermore, an analysis of the trophic basis of production prior to amphibian declines showed that the diets of macroinvertebrates did not change with seasons, indicating that macroinvertebrates are not shifting diets as environmental conditions fluctuate (Frauendorf et al. 2013). These lines of evidence suggest that intra- and interannual variability were unlikely to be driving the changes that we observed in the food web.

Although our results on the structure of the food web suggest that coarse-grained measures of food web structure are resilient to amphibian declines, it remains possible that changes in the weights of linkages may have occurred. Assessing changes to a network with weighted linkages could reveal changes in the dietary preferences of algal-grazing insects, such as mayflies. In

the six months following amphibian declines, algal-grazer richness and abundance declined (Colón-Gaud et al. 2010b). This was accompanied by increased densities of diatoms, a primary resource for algal-grazing insects, and a shift in the diatom community from smaller-bodied diatoms ($<5000 \mu\text{m}^3$) to larger-bodied diatoms ($>5000 \mu\text{m}^3$) (Connelly et al. 2008). This pattern in the grazer and diatom communities continued four years post-decline, with three mayfly genera in riffles and four mayfly genera in pools declining to $<2 \text{ mg AFDM/m}^2$ (Appendices A and B). Using the population changes in the insect-grazer and diatom community as evidence, amphibian declines may have changed the food web by altering the linkage weights within the food web, but this is beyond the scope of this investigation.

Changes in consumer feeding behavior, most notably in the Odonata, played a major role in restructuring the food web (Appendix D). Increased numbers of diatom genera in the guts of odonates occurred in individuals from both riffle and pool habitats. Additionally, there were significant increases in the numbers of diatom valves and filamentous algae (*A. chantransia*) in the guts

of several odonate taxa, indicating that the increased prevalence of diatom genera in odonate guts is unlikely to be due to incidental ingestion or from the gut contents of prey (Appendix D). Moreover, the availability of preferred prey for odonates, such as tadpoles and macroinvertebrates, declined following amphibian declines (Colon-Gaud et al. 2010a; see Appendix A). A dietary shift that includes more algae is not unique, because predatory aquatic insects will consume algae when the abundance of preferred prey decreases (Lancaster et al. 2005). Combined, our data suggest that a major change in the consumer feeding behavior of odonates occurred between 2004 and 2009.

Our betweenness centrality results indicate the difficulty of identifying which taxa will occupy a central position in a food web following species loss. These findings support a conservation strategy that advocates protecting the whole ecosystem (Ives and Cardinale 2004) vs. a strategy that focuses efforts on specific species that occupy central positions in the food web (Tylianakis et al. 2010). The betweenness centrality values of species prior to amphibian declines did not predict which species would become important to the topology of the food web after amphibian declines. Species central to post-decline food web topology were not central to pre-decline food web topology, as taxa exhibiting the highest betweenness centrality values post-decline were unranked pre-decline. Our results indicate that a strategy protecting taxa with high betweenness centrality values would not be effective because it could exclude those taxa that ultimately became central to the food web.

Our findings are consistent with the prediction that food web robustness to species loss, as measured by the number of secondary extinctions following a primary extinction, increases with connectance (Dunne et al. 2002, Eklöf and Ebenman 2006). However, food web studies that use static trophic linkages and do not consider compensation through endogenous change in population size or behavioral adaptation require a species to lose all resources before a secondary extinction occurs (Eklöf and Ebenman 2006). This implies that secondary extinctions are constrained to species at trophic levels higher than the trophic level of the primary extinction. In our study, taxa that went secondarily extinct did not lose all of their resources and many occupied the same trophic level as tadpoles. Food web studies that use static trophic linkages, but include population dynamics, predict more secondary extinctions than models that do not include population dynamics and also predict secondary extinctions to occur at all trophic levels (Eklöf and Ebenman 2006, Curtsdotter et al. 2011). Curtsdotter et al. (2011) explored a large range of scenarios that tested the effects of species loss on food web structure based on characteristics of the primary species that went extinct. These predictions suggested that the loss of the largest species (tadpoles were the largest consumer in our food

web) would cause 0–20% of remaining species to go secondarily extinct, while the loss of a generalist species (tadpoles had the most linkages in the pre-decline food web) would also cause 0–20% of remaining species to go secondarily extinct. In our study system, 25% of species in pools and 15% of species in riffles were secondarily extirpated from the community. These results suggest that the use of a dynamic model might more accurately predict the percentage of secondary extinctions that might occur from a community. However, a dynamic model could predict the extirpation of different species than were actually observed. Comparing the characteristics of species (such as the number of trophic linkages) that were predicted to become extirpated to characteristics of those species that were extirpated might provide further insight into how well dynamical models can predict the effects of a perturbation on food web structure.

Our findings are also consistent with a less common prediction suggesting that food web structure may be determined by basic rules that are independent of community composition. These studies use snapshots to compare food web structure year to year, showing little annual variability in food web structure despite >50% species turnover (Cohen et al. 2009, Kaartinen and Roslin 2012). A similar pattern occurred in stream channels that were subject to drought conditions; changes to the organization of these stream food webs occurred following drought, but connectance did not change, despite overall declines to species richness (Ledger et al. 2013). Our results corroborate the conclusion from these studies that basic rules may structure food webs, a result that is likely to be missed by analyzing aggregated food webs. Our results are also unique because they suggest mechanistic causes underwriting food web resilience. We also used a null model to compare our observed results against our predicted results, further supporting our conclusion that species loss may have a smaller effect on food web structure than that predicted by models with static linkages.

Our results also suggest that nontrophic interactions and indirect effects should be incorporated into analyses of ecological networks to yield better insight into the consequences of changing species composition (Bascompte 2009, Ings et al. 2009). Most of the macroinvertebrates that declined by 2009 were not trophically linked to tadpoles. For example, tadpoles facilitate access to food resources for some taxa through bioturbation, reducing inorganic sediment accrual on stream substrates (Ranvestel et al. 2004). Increased sediment accrual may reduce macroinvertebrate populations by negatively affecting macroinvertebrate mobility and foraging (Connolly and Pearson 2007). Tadpoles also increase the nutritional quality of biofilm through excretion, by reducing biofilm C:N and C:P (Connelly et al. 2008, Ruginski et al. 2012). These examples demonstrate how a species can mediate community composition, even when species are not trophically

linked, directly underscoring the importance of nonconsumptive effects in structuring ecological communities.

In our study stream, several important food web structural attributes were more resilient to species loss than predicted by calculations assuming fixed trophic linkages. The resilience of food web structure appears to have been a function of new linkages that formed after the loss of a dominant taxonomic group, changes in consumer diets, and appearance of “new” generalist taxa that appeared post-decline. Many studies that examine effects of species loss on food web structure assume that food web structure is only shaped by the original trophic linkages. However, our study suggests that dynamic trophic interactions and indirect effects may serve an important role in structuring food webs after species loss, providing support for the hypothesis that food web structure is shaped by factors independent of their original trophic linkages.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D are available online: <http://dx.doi.org/10.1890/14-1526.1.sm>