



Bottom-up influences on tropical freshwater food web structure support the “environmental filtering” hypothesis

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Abstract

Studies of ecosystem functions are gaining traction in the scientific community along with a growing consensus that losses in ecosystem functions have widespread consequences. Food webs, which are networks comprising all trophic interactions (represented by links) between taxa present in a community (represented by nodes), are important aspects of ecosystem functioning, yet a clear understanding of the factors and mechanisms influencing their assembly and structure is lacking. In our study, we addressed this fundamental question by investigating the respective roles of (1) environmental filtering and (2) biotic filtering, in governing food web structure. We did this by assessing the relationship between the network structure of five high-resolution empirical tropical food webs and associated environmental and biotic covariates. Our data suggest that only environmental filtering is important in shaping food webs. Further, we found that the underlying ecological mechanism is a function of bottom-up influences comprising resource levels, and to a lesser degree, resource type (i.e., terrestrial organic matter) available. Specifically, our data suggest high-nutrient environments favor greater food web complexity. In the general context of community assembly, our findings add to existing knowledge of the process by demonstrating that environmental conditions previously shown to influence species assemblages can also drive trends in prevailing species interactions.

Nearly unprecedented losses in biodiversity resulting from anthropogenic activities (Caballos et al. 2015) have driven a shift to pragmatic conservation efforts where emphasis is placed on the preservation of ecosystem functions (Cadotte et al. 2011; Flynn et al. 2011). This is in part, the result of a growing consensus that loss of ecosystem functions can have widespread consequences for biodiversity and humans alike (Midgley 2012; Gamfeldt et al. 2014; Duncan et al. 2015). The robustness of ecosystem functioning depends on a range of factors including diversity of functions (Cadotte et al. 2011; Flynn et al. 2011) and trophic interactions (Duffy et al. 2007; Thompson et al. 2012).

Disruptions to key trophic interactions can impact ecosystem functions such as carbon cycling and net primary

productivity (Holt and Loreau 2001). However, there is much we are yet to fully understand about food webs (i.e., networks comprising all trophic interactions between taxa present in a community), including the fundamental subject of identifying drivers (biotic and environmental) and mechanisms which influence the realization of certain sets of trophic interactions over others (i.e., food web assembly; May 2009).

To date, most of what we know about food web assembly comprises mathematical assembly rules which predict food web structure (i.e., network topology) as a function of mathematical constraints (e.g., the Lotka–Volterra equation; Haerter et al. 2016). By demonstrating that the formation of predator–prey interactions can be governed by body-size dependent hierarchies, seminal publications by Elton (1927) and Cohen et al. (1985), among others, added a biological dimension to food web assembly. These assembly rules have since proven helpful in constructing theoretical food web models (Dunne and Williams 2009; Romanuk et al. 2017).

Food web assembly is rarely investigated empirically and knowledge about the process is instead inferred from focused studies (Bukovinszky et al. 2008; Layer et al. 2010; Okuda et al. 2017). For example, Layer et al. (2010) documents a predictive relationship between pH and the complexity (i.e., connectance)

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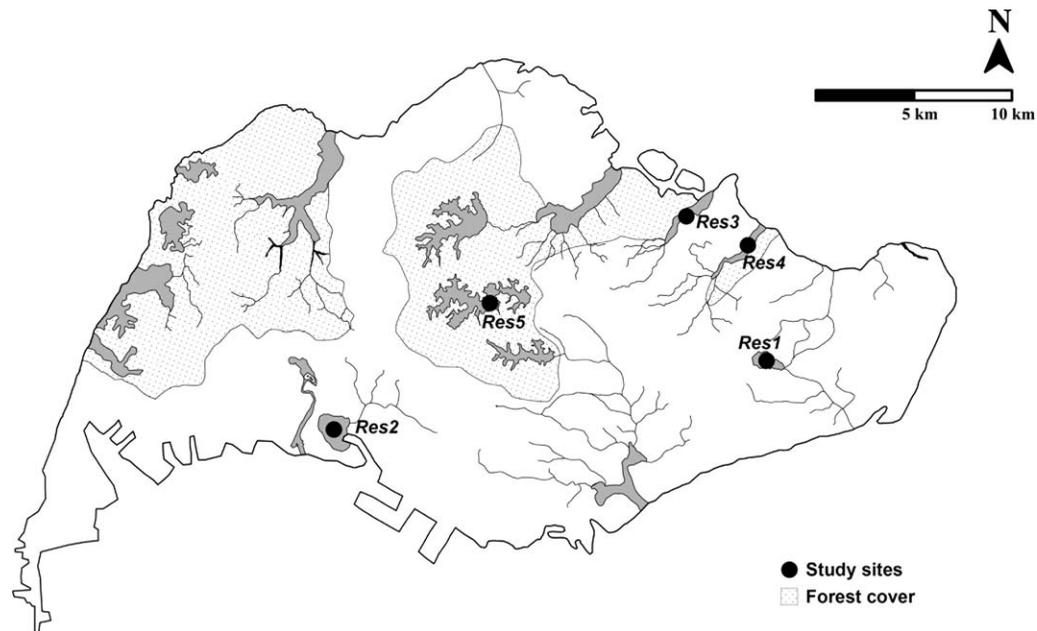


Fig. 1. Map of study sites surveyed.

of aquatic food webs while Bukovinszky et al. (2008) demonstrates that resource quality influences the structure of simple host-parasitoid-secondary parasitoid food webs. In addition to environmental variables, biological factors (e.g., species composition) also influence some aspects of trophic ecology, albeit in an indirect or intermediary role (Cole et al. 2000). By piecing the available empirical data together, we may speculate that both environmental and biological variables play integral roles in food web assembly. However, nuances in the nature of the relationships may lead to spurious conclusions. Moreover, efforts to characterize the process of food web assembly using existing literature are confounded by incongruent approaches between empirical and theoretical studies. While theoretical food web literature addresses potential determinants of network topology at a community level (e.g., connectance, link density; Dunne and Williams 2009), literature measuring empirical predictors of food web structure often quantify differences (or changes) in the relative proportion of functional groups of interest (Post et al. 1997; Baden et al. 2012).

Food web assembly bears many parallels to the assembly of species communities (or simply community assembly) and the two are sometimes conflated (Hall and Raffaelli 1993). The latter, however, is better understood and this is evident in the extensive body of literature documenting the influence of both environmental and biological variables on species assemblage (Hille Ris Lambers et al. 2012). Mechanistically, environmental conditions influence species assemblages by favoring the colonization/establishment of suites of species adapted to similar environments or with similar biogeographical histories (Kraft et al. 2015; Giam and Olden 2016). Biological factors, on the other hand, govern

community assembly via interspecific interactions (e.g., competition and predation may preclude the colonization/establishment of some species) (Kraft et al. 2008; Giam and Olden 2016). Descriptions of the influence of environmental and biological factors on community assembly are referred to as the environmental filtering (Kraft et al. 2015) and biotic filtering (Giam and Olden 2016) hypotheses, respectively.

Considering the similarities with community assembly, we tested the cogency of the environmental filtering and biotic filtering hypotheses in shaping food web structure. This was done by analyzing the network topology (or structure) of high-resolution empirical food webs (constructed using a combination of gut/stomach content as well as stable isotope data) in response to a range of environmental and biological variables. We sampled five freshwater communities in tropical East Asia, an area that is subject to intense anthropogenic stress, yet remains understudied (Sodhi et al. 2004). Using the data collected, we asked if food web structure is governed by environmental filtering, biotic filtering, or both? With the use of path analysis, we also characterized the probable ecological mechanism underlying food web assembly.

Methods

Description of study sites

We surveyed five man-made lentic habitats in the tropical island nation of Singapore (1.35° N, 103.82° E; Fig. 1). Our study sites consisted of highly accessible urban reservoirs (*Res1* and *Res2*) with relatively vegetation-free riparian zones, as well as impounded rivers with riparian matrices ranging from bare rocky bunds to dense secondary forest vegetation (*Res3* and *Res4*), and one protected reservoir located within a

nature reserve (*Res5*). These water bodies range in age from 6 to 45 years and they represent a novel habitat type absent in primeval Singapore (Yeo and Lim 2011; Supporting Information Appendix D). Fish communities at the sites comprised both native and introduced species with eclectic biogeographic origins (Ng and Tan 2010). All five sites are warm (water temperature between 27.4°C and 31.0°C), slightly basic (pH between 7.20 and 8.90), and relatively turbid (secchi depth between 0.4 m and 2.0 m).

Sample collection

All specimens were collected from January 2014 to February 2016. While we were not able to sample the sites concurrently, we are confident that our sampling regime was sufficiently representative considering that temporal fluctuations in trophic interactions are relatively minor (even when subjected to comparatively large subtropical variations in climatic conditions; Lau et al. 2009).

The coverage of communities sampled were maximized by collecting the following groups of organisms: (1) primary producers (i.e., riparian plants, riparian grasses, phytoplankton, and periphyton); (2) invertebrates (e.g., zooplankton, dipterans, ostracods, decapods, and gastropods); and (3) fishes (i.e., all fish species occurring at each site). Primary producers were sampled via leaf clipping of numerically dominant taxa (i.e., for riparian plants and grasses), horizontal trawls with nets of mesh size 80 μm (i.e., for phytoplankton via seston samples), and scraping of submerged rocky surfaces (i.e., for periphyton). Invertebrate specimens were collected with submerged colonizers deployed at a fixed depth of 1 m over a 1-month period (i.e., for benthic invertebrates; Loke et al. 2010) and by conducting horizontal trawls with nets of 80 μm mesh sizes (i.e., for planktonic invertebrates). We collected fishes using a combination of cast netting, trapping, and electrofishing. All specimens were identified and analyzed at the highest taxonomic resolution possible (i.e., family level for invertebrates and species level for fish).

Construction of empirical food webs

We applied both stable isotope analysis (SIA) and gut content analysis (GCA) to complement each other and to account for their respective limitations (see e.g., Li and Dudgeon 2008; Dudgeon et al. 2010; Davis et al. 2012).

Gut content analysis

Specimens were euthanized upon collection in a 250 mgL^{-1} MS-222 solution (Institutional Animal Care and Use Committee of the National University of Singapore, Protocol number B13-4690). We restricted our analyses to contents found in the foreguts (i.e., stomach) of specimens collected. While we identified all food items to the highest resolution possible, this was not always feasible for contents in advanced stages of digestion. Therefore, the pool of potential food items assessed using SIA data sometimes include morphologically similar taxa. For example, gobioid fishes

Rhinogobius giurinus and *Pseudogobiopsis oligactis* were analyzed concurrently as potential prey when syntopic, even if only one of the two was observed in the gut/stomach contents of a predatory taxon. To prevent overlooking any trophic interactions, we adopted a highly inclusive approach, where single occurrences (across all five reservoirs) warranted inclusion as a potential food item in mixing models.

Stable isotope analysis

For producers, we analyzed: (1) leaf clippings of riparian plants and grasses, (2) filtered and concentrated phytoplankton cells/colonies, and (3) substrate-free periphyton tissue. In larger invertebrates (i.e., gastropods and decapods), we extracted muscle tissue for SIA, while samples of small invertebrates (e.g., zooplankton and dipteran larvae) consisted of pooled, whole specimens. For all fish specimens, we extracted and processed muscle tissue from the dorsal region. We were limited by our inability to achieve greater resolution for planktonic and bacterial components of the food webs. Difficulties in obtaining requisite sample weights for smaller organisms (i.e., ≈ 1 mg dry-weight) necessitated the use of plankton nets of larger mesh size more suited for horizontal trawls over long distances (i.e., ≈ 100 m). To minimize potential confounders and/or biases stemming from the underrepresentation of smaller planktonic taxa (e.g., rotifers), we standardized our collection protocol across all study sites.

All samples were oven-dried for 48–72 h at 68.5–70.0°C, homogenized, weighed (to the nearest 0.0001 g), and packed in standard tin capsules to be sent to the Stable Isotope Facility at the University of California, Davis for analyses (see Supporting Information Appendix A).

We used SIA data to quantify the relative strengths of all trophic relationships with Bayesian mixing models on the *SIAR**4.2 statistical package (Parnell and Jackson 2013). For every consumer taxon, we ran 500,000 iterations (burn-in = 50,000) of dual element (i.e., $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) concentration dependent models. Taxon-specific $\delta^{15}\text{N}$ trophic discrimination factors ($\Delta^{15}\text{N}$) were applied to account for the taxonomic diversity included in our analyses. For primary producer and invertebrate sources, we used $\Delta^{15}\text{N}$ values from Bunn et al. (2013) (i.e., $\Delta^{15}\text{N} = 0.6 \pm 1.7\text{‰}$ for herbivorous invertebrates, $\Delta^{15}\text{N} = 1.8 \pm 1.7\text{‰}$ for carnivorous invertebrates feeding on herbivorous invertebrates, and $\Delta^{15}\text{N} = 4.3 \pm 1.5\text{‰}$ for omnivorous fish feeding on primary producers), while $\Delta^{15}\text{N}$ for vertebrate prey were adapted from McCutchan et al. (2003) (i.e., $\Delta^{15}\text{N} = 3.3 \pm 0.3\text{‰}$). Further, we also corrected $\delta^{13}\text{C}$ values for trophic discrimination ($\Delta^{13}\text{C} = 0.4 \pm 1.3\text{‰}$; Post 2002) and lipid enrichment (after Logan et al. 2008). In all mixing models, we confirmed the presence of all potential food sources by ensuring that consumer isotopic profiles were bounded within mixing polygons (Phillips et al. 2014). Model outputs were summarized with medians of the posterior distribution of source-contribution values so each food source (per consumer taxon) was represented by a single source-contribution percentage (Supporting Information Appendix H).

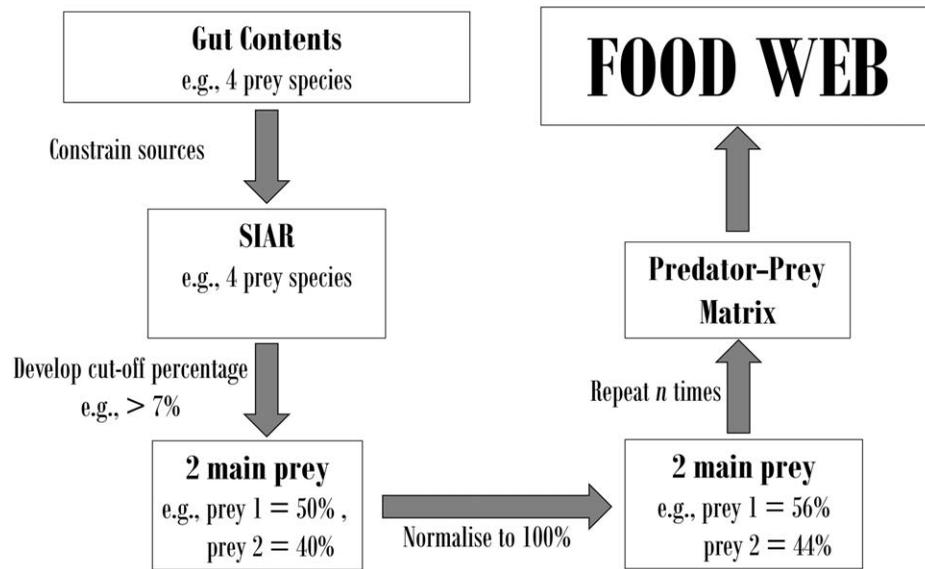


Fig. 2. Flow-chart detailing the stepwise procedure involved in constructing our empirical food webs. Values in the chart are hypothetical representations of a consumer species in a food web with n consumer taxa.

Food web construction

Outputs from GCA and SIA were combined to construct empirical food webs in a stepwise procedure (Fig. 2). First, we identified major prey items in the guts of consumer taxa (described in GCA subsection) to constrain potential food sources analyzed with mixing models (described in the SIA subsection). Second, we removed less ecologically important (or stochastic) predator–prey relationships (i.e., food items with median proportion source contributions values of ≈ 0). Third, we standardized source contribution proportions of remaining food sources by normalizing the values to sum to 100%. To this end, the following formula was applied:

$$\text{Normalized source contribution} = \frac{\text{Source contribution of } j\text{th source}}{\sum (\text{Source contribution of major food sources})} \times 100$$

Finally, we repeated the previous steps for all consumer taxa (n) present in a community and the normalized source contributions were collated in a predator–prey matrix (Supporting Information Appendix I). This process was applied to all five food webs analyzed.

The food webs were visualized with *igraph**1.01 (Csardi and Nepusz 2006). Here, nodes, representing constituent taxa, were ordered along the vertical axis of the webs using respective trophic levels which we calculated with the *NetIndices**1.4.4 statistical package (Kones et al. 2009). We summarized all five webs with network topology indices representing ecologically relevant characteristics of their structure: (1) connectance (i.e., measure of overall complexity reflected in fraction of realized links over total possible links; Dunne et al. 2002a); (2) maximum trophic level (i.e.,

measure of vertical complexity reflected in the highest trophic level occupied by a consumer in the food web; Digel et al. 2014); (3) mean index of omnivory (i.e., measure of vertical complexity represented by average variation in trophic levels of prey items consumed by all heterotrophic taxa; Thompson et al. 2007); (4) mean trophic level (i.e., measure of vertical distribution of taxa in the food web reflected in the average trophic level; Digel et al. 2014); and (5) Gini's coefficient (i.e., measure of evenness in the distribution of trophic interaction strengths with upper and lower limits of zero and one, respectively, where a value of zero reflects perfect equivalence of interaction strength among links in the food web; van Altena et al. 2016).

Assessment of food web assembly hypotheses

To assess the importance of biotic and environmental filtering in shaping food web structure, we tested for statistical trends in measures of food web structure in relation to biological and environmental predictors (Table 1). This was done by comparing the pairwise dissimilarity of food web structure with pairwise dissimilarity of functional assemblage and environmental variables for all possible combinations of the five aquatic communities surveyed ($n = \binom{5}{2} = 10$).

Enumeration of dissimilarity indices

The response variable in our analysis, pairwise dissimilarity of food web structure (FW_{dis}), was calculated by computing Euclidean distances of the food web structures represented by scaled network topology indices (i.e., connectance, maximum trophic level, mean index of omnivory, mean trophic level, and Gini coefficient).

To test the biotic and environmental filtering hypotheses, we calculated two predictor variables. Biotic filtering was

Table 1. Inferential framework describing predictor variables associated with the environmental filtering and biotic filtering hypotheses, respectively. The prediction column describes expected outcomes should our data support either hypothesis (or both hypotheses).

Hypothesis	Description	Variables	Prediction
Biotic filtering	Food web structure is governed by mechanistic processes influenced by the functional assemblage. An increase in functional similarity would mean a concomitant increase in overlaps of realized trophic niches and links, giving rise to structurally similar food webs.	(1) Feeding guild; (2) trophic index; (3) body size; (4) trophic breadth; (5) position occupied in water column; (6) body shape; (7) fecundity/population doubling time.	Pairwise dissimilarity of food web structure (FW_{dis}) would increase with increasing dissimilarity in functional assemblage (FN_{dis}).
Environmental filtering	Food web structure is governed by mechanistic processes driven by the environment. Shared physical and/or chemical traits in a habitat are likely to result in similarities in availability of biological niches which favors the formation of a specific set of trophic interactions. This would then be reflected in similarities in food web structure.	(1) Riparian tree cover density; (2) habitat surface area; (3) habitat perimeter; (4) pH; (5) levels of dissolved oxygen; (6) levels of total dissolved solids; (7) levels of organic nitrogen (i.e., total nitrogen, total ammonia, total nitrate, total nitrite).	Pairwise dissimilarity of food web structure (FW_{dis}) would increase with increasing dissimilarity in environmental variables (E_{dis}).

represented by mean dissimilarity in functional assemblages (FN_{dis}) comprising the following functional traits for all the fish species present in all communities sampled (Supporting Information Appendix B): (1) functional guild (nominal variable with four levels; detritivore, omnivore, invertivore, and predator); (2) trophic index (continuous variable representing average dietary composition reported in literature, where greater values suggest increasing carnivory); (3) body size (continuous variable representing maximum body size recorded in respective study sites); (4) trophic breadth (ordinal variable between one and seven reflecting the number of food items occurring in a species' diet; these food items are comprised of detritus, plant matter, phytoplankton, periphyton, zooplankton, macroinvertebrates, and fishes); (5) position occupied in the water column (nominal variable with three levels; demersal, benthopelagic, and pelagic); (6) body shape (continuous variable represented by a length-weight parameter describing the body shape of a fish species); and (7) fecundity (nominal variable with four levels; high, medium, low, and very low). With the exception of trophic breadth (inferred from GCA) and body size, data for all other variables were collated from Fishbase (Froese and Pauly 2011; Supporting Information Appendix C). We were limited by our inability to include nonfish taxa in the calculation of FN_{dis} owing to the absence of species level taxonomic expertise, as well as a general paucity of functional data pertaining to invertebrate consumers. Because functional trait data were a mix of continuous, ordinal, and nominal variables, interspecific functional dissimilarity was represented by Gower's distance (Gower 1971). We calculated pairwise mean functional dissimilarity between all possible pairs of community

assemblages using the following formula: $FN_{dis} = \frac{\sum_i^{mm} FN_{dis,i}}{mm}$, where $FN_{dis,i}$ represents the i th species pair from communities with n and m consumer taxa, respectively.

Environmental filtering was represented in our analyses by environmental dissimilarity (E_{dis}). We derived this by calculating Euclidean distances of the following environmental variables between all possible pairs of communities: (1) riparian tree cover density (continuous variable ranging from 1 to 100 signifying percentage of riparian zones within 100 m of the water's edge with significant forest vegetation cover); (2) habitat surface area (continuous variable signifying surface area of habitat surveyed in km^2); (3) habitat perimeter (continuous variable representing total perimeter of habitats surveyed in km); (4) pH level (continuous variable representing mean pH levels associated with a habitat); (5) levels of dissolved oxygen (continuous variable representing mean levels of dissolved oxygen associated with a habitat in mgL^{-1}); (6) levels of total dissolved solids (continuous variable representing mean levels of total dissolved solid associated with a habitat); and (7) nutrient levels (four separate continuous variables representing levels of total nitrogen, ammonia, nitrate, and nitrite in mgL^{-1} ; Table 1). Physical environmental variables (1)–(3) were calculated using the QGIS*2.18 geographic information system (Hansen et al. 2013; QGIS Development Team 2014; see Supporting Information Appendix B), while chemical variables (4)–(6) were measured with a YSI multiparameter probe over 40 sampling occasions, and nutrient data (7) was obtained via Singapore's water agency (PUB). All dissimilarity indices (i.e., FW_{dis} , FN_{dis} , and E_{dis}) were enumerated using the *vegan* statistical package (Oksanen et al. 2013).

Table 2. List of models tested in an information theoretic framework and their respective interpretations.

	Model	Model interpretation
Null Model	$FW_{\text{dis}} \sim 1$	Pairwise dissimilarity of food web structure is not associated with pairwise dissimilarity of community functional assemblage or environmental variables. This suggests that neither biotic nor environmental filtering are relevant in shaping food webs.
Model 1	$FW_{\text{dis}} \sim FN_{\text{dis}}$	Pairwise dissimilarity in food web structure is only associated with pairwise dissimilarity of community functional assemblage. This suggests that only biotic filtering is important in shaping food webs.
Model 2	$FW_{\text{dis}} \sim E_{\text{dis}}$	Pairwise dissimilarity in food web structure is only associated with pairwise dissimilarity of environmental variables. This suggests that only environmental filtering is important in shaping food webs.
Model 3	$FW_{\text{dis}} \sim FN_{\text{dis}} + E_{\text{dis}}$	Pairwise dissimilarity in food web structure is associated with pairwise dissimilarity of community functional assemblage and environmental variables. This suggests that both biotic and environmental filtering are important in shaping food webs.
Model 4	$FW_{\text{dis}} \sim FN_{\text{dis}} \times E_{\text{dis}}$	Pairwise dissimilarity in food web structure is predicted by the interaction between pairwise dissimilarity of community functional assemblage and environmental variables. This suggests that the influence of biotic and environmental filtering on food web structure are not independent of each other.
Model 5	$FW_{\text{dis}} \sim e^{FN_{\text{dis}}}$	Pairwise dissimilarity in food web structure changes exponentially with increasing pairwise dissimilarity of community. This suggests that biotic filtering is important in shaping food webs and differences in functional assemblages have an exponential influence on food web structure. In this notation, e represents the mathematical constant Euler's number.
Model 6	$FW_{\text{dis}} \sim e^{E_{\text{dis}}}$	Pairwise dissimilarity in food web structure changes exponentially with increasing pairwise dissimilarity of environmental variables. This suggests that environmental filtering is important in shaping food webs and differences in environmental variables have an exponential influence on food web structure. In this notation, e represents the mathematical constant Euler's number.

Statistical analyses

We tested the statistical relationship between our response variable (i.e., FW_{dis}) and both predictor variables (i.e., FN_{dis} and E_{dis}) in an information theoretic framework (Table 2). These consisted of Bayesian generalized linear models which, unlike equivalent frequentist approaches, are not constrained by assumptions of large sample sizes (Kery 2010). From the list of competing models, we selected the model best describing our data (i.e., greatest parsimony). The models were constructed with the *rjags* statistical package (Bates et al. 2012) where posterior distribution of model coefficients were determined with 500,000 iterations on four chains (thinning interval = 1). We assessed relative model parsimony by calculating deviance information criterion (DIC) (thinning interval = 20) (Spiegelhalter et al. 2014). Here, lower DIC scores suggest greater parsimony. Further, we evaluated model fit using adjusted R^2 (R^2_{adj}) obtained via comparisons between model predictions and observed data (after Giam et al. 2015). Pairwise data can sometimes result in the inflation of the likelihood of Type 1 errors (i.e., incorrect rejection of a true null hypothesis). Therefore, we verified the outcome of our analyses by adopting a “leave-one-out” approach where analyses are repeated with data subsets consisting of only four (out of five) study sites. This was conducted iteratively with all possible data subsets (i.e., total of five, with one nonrepeated study site removed in each data subset, respectively) to identify potential site-specific confounders.

In addition to identifying the relative importance of biotic and/or environmental filtering in shaping food web structure,

we also elucidated the underlying ecological mechanisms by assessing candidate Bayesian structural equation models (SEMs) describing a set of plausible hypotheses (Supporting Information Appendix E). Here, we tested the relationship between FW_{dis} and the constituent components of FN_{dis} and E_{dis} , in the event that either (or both) are shown to be statistically significant. For FN_{dis} , the components were (1) trophic ecology (i.e., feeding guild, trophic index, and trophic breadth); (2) physical characteristics (i.e., body size and body shape); and (3) habitat preference (i.e., position occupied in water column). Components of E_{dis} were (1) physical habitat characteristics (i.e., habitat surface area and habitat perimeter); (2) riparian tree cover density; (3) water chemistry (i.e., pH, levels of dissolved oxygen, and levels of total dissolved solid); and (4) nutrient levels (i.e., total nitrogen, total ammonia, total nitrate, and total nitrite). For each of the constituent components, we again calculated pairwise dissimilarity indices in all possible community pairs ($n = 10$). We used Gower's distance to enumerate dissimilarity in components with both nominal and continuous variables (e.g., trophic ecology), while pairwise dissimilarity of components consisting entirely of continuous variables (e.g., physical habitat characteristics) were estimated using Euclidean distances. Similarly, relative model parsimony was assessed using DIC values.

Results

Empirical food webs and their network structure

Across the five food webs studied, we encountered a total of 29 fish species (Supporting Information Appendix C) and

Table 3. Network topology indices of the food webs of the five tropical communities studied.

Site	Taxa richness	Connectance	Maximum trophic level	Average trophic level	Index of omnivory	Gini coefficient
Res1	25	0.14	4.62	2.66	0.16	0.33
Res2	23	0.17	4.34	2.64	0.14	0.35
Res3	23	0.18	4.63	2.88	0.21	0.28
Res4	25	0.17	4.61	2.81	0.38	0.32
Res5	22	0.20	4.54	2.64	0.23	0.31

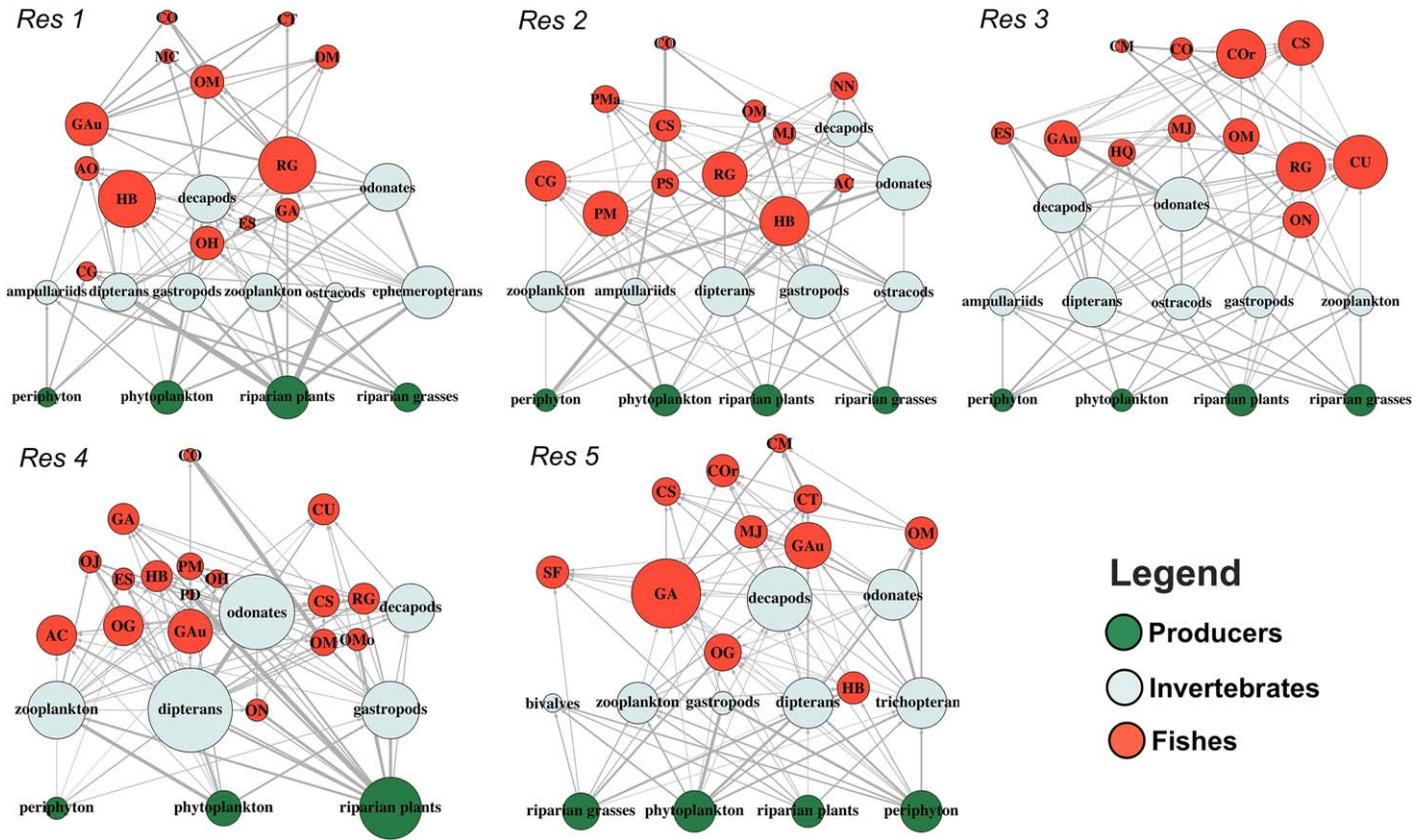


Fig. 3. Graphical representations of empirical food webs of five lentic communities. The size of each node (representing individual taxa) in the food web reflects the number of links formed by each taxon, while the thickness of arrows (representing predator–prey relationships) represent the relative strength of the trophic interactions. Directions of arrows are from prey to predator. Abbreviations in the webs denote the following fish species: AC, *Amphilophus citrinellus*; AO, *Astronotus ocellatus*; CG, *Clarias gariepinus*; CM, *Channa micropeltes*; CO, *Cichla orinocensis*; COOr, *Chitala ornata*; CS, *Channa striata*; CT, *Cichla temensis*; CU, *Cichlasoma urophthalmum*; DM, *Datnioides microlepis*; ES, *Etroplus suratensis*; GA, *Geophagus altifrons*; GAu, *Glossogobius aureus*; HB, *Heterotilapia buttkoferi*; HQ, *Hyporhamphus quoyi*; MC, *Megalops cyprinoides*; MJ, *Monopterus javanensis*; NN, *Notopterus notopterus*; OG, *Osphronemus goramy*; OH, *Oreochromis hybrid*; OJ, *Oryzias javanicus*; OM, *Oxyeleotris marmorata*; OMo, *Oreochromis mossambicus*; ON, *Oreochromis niloticus*; PD, *Pterygoplichthys disjunctivus*; PM, *Paraneotroplus melanurus*; PMa, *Parachromis managuensis*; PS, *Parambassis siamensis*; RG, *Rhinogobius giurinus*; SF, *Scleropages formosus*.

one hybrid (i.e., *Oreochromis mossambicus* × *Oreochromis niloticus*). Structures of the five food webs varied in complexity with connectance values ranging between 0.14 and 0.20, and mean index of omnivory ranging between 0.14 and 0.38 (Table 3; Fig. 3). Conversely, maximum trophic levels recorded were relatively uniform across the five food webs, ranging from 4.34 (i.e., Res2) to 4.63 (i.e., Res3), and this was

also the case for mean trophic levels (i.e., 2.64–2.88). All food webs had relatively even distributions of interaction strength (i.e., Gini’s coefficient: 0.28–0.35).

Roles of environmental filtering and biotic filtering

From the list of candidate linear models describing the relationship between FW_{dis} and both predictor variables

Table 4. Output of model comparisons in an information theoretic framework. Model parsimony and fit are represented by DIC and adjusted R^2 (R^2_{adj}) values, respectively. Posterior distributions of coefficients associated with their respective predictor variables are represented by mean and 95% credible intervals (in parentheses). Nonzero outcomes (i.e., 95% CI does not overlap with 0) suggest statistical significance.

	Model	DIC	R^2_{adj}	Coefficient values
Null model	$FW_{\text{dis}} \sim b_0$	5.05	NA	$b_0 = 0.48$ (0.28, 0.67)
Model 1	$FW_{\text{dis}} \sim b_0 + b_1 FN_{\text{dis}}$	7.25	-0.05	$b_0 = 1.78$ (-2.28, 6.69) $b_1 = -3.31$ (-15.66, 6.94)
Model 2	$FW_{\text{dis}} \sim b_0 + b_1 E_{\text{dis}}$	1.68	0.42	$b_0 = -0.26$ (-0.94, 0.42) $b_1 = 0.35$ (0.04, 0.65)
Model 3	$FW_{\text{dis}} \sim b_0 + b_1 FN_{\text{dis}} + b_2 E_{\text{dis}}$	0.05	0.65	$b_0 = 2.22$ (-1.98, 7.91) $b_1 = -6.56$ (-21.59, 4.27) $b_2 = 0.40$ (0.05, 0.71)
Model 4	$FW_{\text{dis}} \sim b_0 + b_1 FN_{\text{dis}} + b_2 E_{\text{dis}} + b_3 FN_{\text{dis}} \times E_{\text{dis}}$	4.42	0.16	$b_0 = 7.44$ (-1.35, 19.98) $b_1 = -20.47$ (-53.72, 2.98) $b_2 = -1.84$ (-7.72, 2.54) $b_3 = 5.99$ (-5.47, 21.36)
Model 5	$FW_{\text{dis}} \sim b_0(e^{b_1 FN_{\text{dis}}})$	20.75	-0.04	$b_0 = 2.52 \times 10^{-19}$ (6.44×10^{-88} , 2.26×10^{12}) $b_1 = -18.99$ (-193.20, 136.49)
Model 6	$FW_{\text{dis}} \sim b_0(e^{b_1 E_{\text{dis}}})$	30.17	0.04	$b_0 = 1.51 \times 10^{-9}$ (2.52×10^{-76} , 6.91×10^{25}) $b_1 = -24.07$ (-95.90, 16.70)

(Table 2), Model 3 was best supported by our data (lowest DIC, $R^2_{\text{adj}} = 0.65$) (Table 4). The most parsimonious model comprised both FN_{dis} and E_{dis} , but only the latter was shown to be a statistically significant predictor of food web structure (95% CI does not overlap with zero). Further, the (E_{dis}) coefficient value was positive (95% CI: 0.05–0.71) and this is consistent with one of the two hypothesized outcomes (Table 1). Our observations suggest environmental filtering is important in shaping food webs but some variation in food web structure is also explained by functional assemblages.

Mechanisms underlying environmental filtering

We compared the DIC values of 51 candidate Bayesian SEMs (Supporting Information Appendix E) describing the relationship between FW_{dis} and constituent components of E_{dis} . Our data best supported the SEM in which dissimilarities in nutrient level and riparian tree cover density were modelled as independent predictors of FW_{dis} (Fig. 4b). However, among the two E_{dis} components, only nutrient level was attributed with a nonzero coefficient (i.e., 95% CI: 0.23–0.42). Further scrutiny of our data reveals that nutrient levels in the environment were positively correlated with food web complexity (i.e., connectance and mean index of omnivory), as well as maximum and mean trophic levels (Supporting Information Appendix F). Food webs in high nutrient environments were also associated with greater evenness in the distribution of trophic interaction strengths (i.e., low Gini's coefficient).

Discussion

Our study augments the relatively sparse published literature of empirical food webs from the tropics (Cohen 2010; Thompson et al. 2012; Blanchette et al. 2013). In terms of network topology, indices associated with our lentic food webs were well within published ranges (Pawar 2009; Cohen 2010; Thompson et al. 2012). This was true even when compared with freshwater communities from nontropical climatic regimes, marine communities, and even some terrestrial food webs (Dunne et al. 2002a; Pawar 2009; Thompson et al. 2012).

Findings reported in our study are consistent (at least superficially) with the highly influential, albeit controversial hypothesis (Polis 1991) which posits that food web structures are relatively constant (Martinez 1992). In these earlier studies, connectance values were shown to be scale-invariant, ranging from ~ 0.05 to 0.30 (Dunne et al. 2002a), and converging at a mean of 0.14 (Martinez 1992). This was attributed to the “complexity-stability” trade-off where violations of critical upper limits of realized trophic links result in structural volatility (May 1972; Brose et al. 2003). However, mounting evidence against “constant connectance” (Riede et al. 2010) and the “complexity-stability” paradigm (Valdovinos et al. 2010; Plitzko et al. 2012) has since led to a growing consensus that food web structure is more fluid than previously assumed. This foundational shift in food web theory is partly driven by the discovery of previously overlooked roles of consumer-specific adaptive traits (e.g., in foraging and allometry) in maintaining stability in high

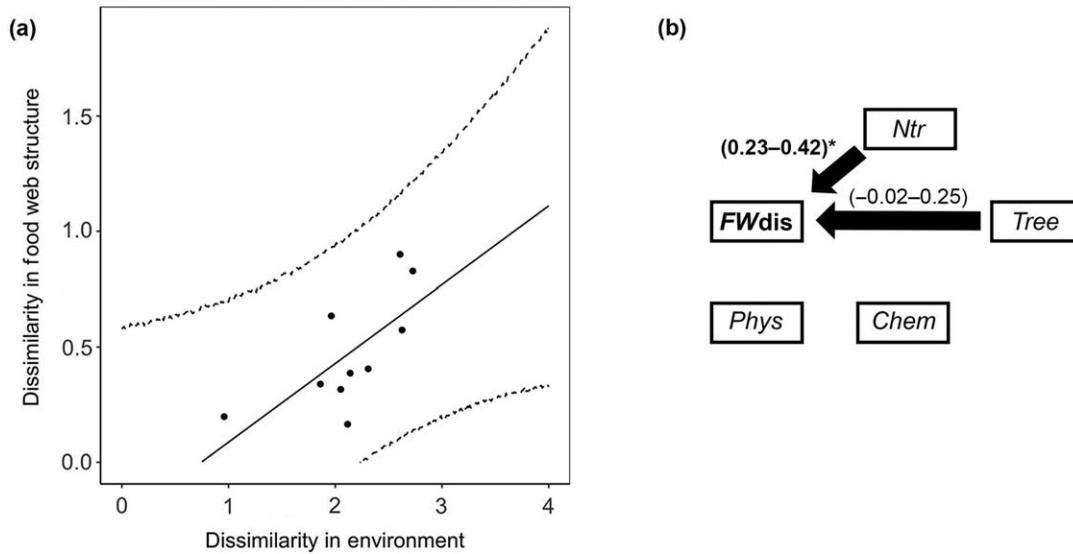


Fig. 4. (A) Relationship between dissimilarity in food web structure (FW_{dis}) and relationship with dissimilarity (E_{dis}). Mean predicted values are represented by the solid line while dashed lines demarcate 95% prediction intervals (i.e., 2.5% and 97.5% quantiles), and filled circles indicate observed values. (B) Graphical representation of SEM best supported by our data describing the statistical relationship between FW_{dis} and two (of four possible) constituents of E_{dis} (i.e., dissimilarity in nutrient levels [Ntr], dissimilarity in riparian tree cover density [$Tree$]). Values associated with each arrow represent 95% CI of respective coefficients and numbers in bold reflect CI ranges that do not overlap with zero.

complexity networks (Uchida et al. 2007; Heckmann et al. 2012).

Drivers of food web assembly

For either of our competing hypotheses (i.e., biotic filtering and environmental filtering) to be true, our data must suggest that variability in food web structure can be explained by external factors and this is congruent with the more nuanced contemporary food web theory (Uchida et al. 2007; Riede et al. 2010; Heckmann et al. 2012). Here, we found that only environmental (and not biotic) filtering is important in shaping food web structure, although some of the variance in food web data is accounted for by differences in functional assemblages. Mechanistically, environmental filtering influences food web structure via nutrient levels and riparian tree cover density but only the former had a significant (nonzero) predictive relationship. This implies that assuming similar relative resource type dominance (i.e., delivery of terrestrial organic matter inferred from riparian tree cover density), resource availability (i.e., nutrient level) shapes patterns of trophic interactions in a bottom-up direction.

The agency of environmental filtering in food web assembly that we propose in this study is consistent with existing knowledge about the effects of resource type and availability on aquatic communities. Prominent ecological theories based on similar logic include the “river continuum concept” (Vannote et al. 1980) and the “alternate stable states hypothesis” (Petraitis and Latham 1999). While previous attempts to link food web ecology with these hypotheses met with mixed outcomes (Rosi-Marshall and Wallace 2002;

Chase 2003), our findings corroborate and augment the existing literature by demonstrating for the first time that environmental variables do not only influence specific aspects of trophic ecology (e.g., proportion of various functional groups; Baden et al. 2012), but also its overall structure (i.e., network topology). Moreover, we show that the influence of environmental filtering extends beyond the microhabitat spatial scale (see Bukovinszky et al. 2008).

Between resource type dominance and resource availability, effects of the latter on food web structure were clearer (Fig. 4b). The positive relationship between resource availability and measures of food web complexity (e.g., connectance and levels of omnivory; Supporting Information Appendix F) aligns with theoretical predictions of adaptive foraging (Uchida et al. 2007). Specifically, abundant resources can promote higher biomasses in a wide range of potential prey items (e.g., periphyton, algivorous primary consumers; Cardinale et al. 2009; Nelson et al. 2013), thus facilitating adaptive prey-switching (*sensu* Uchida et al. 2007) evident in higher densities of trophic interactions (i.e., connectance) with prey of varying trophic levels (i.e., degree of omnivory). In bridging our empirical observations with food web theory, the findings presented here imply that resource availability favors greater structural complexity by facilitating adaptive feeding strategies.

The relationship between resource availability and maximum trophic level is more direct and uncontroversial as upper limits to maximum trophic levels are often the consequence of diminishing resource availability with each trophic step. Therefore, increased resource availability at the

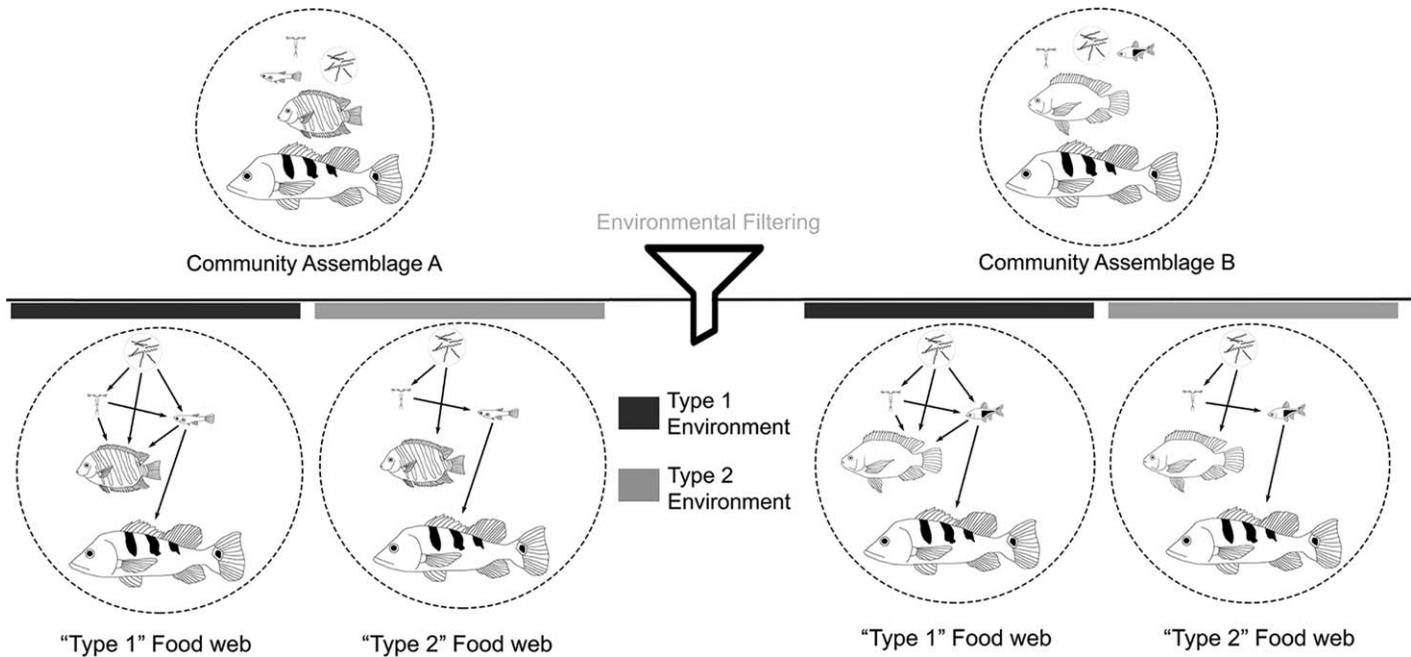


Fig. 5. Graphical summary of the role of environmental filtering in food web assembly.

bottom of the food web allows for the formation of a greater number of trophic transfers before all the energy in the system is lost to entropy (Doi et al. 2009; Takimoto and Post 2013). Similarly, average trophic level would be elevated if resources available to taxa higher up the food web are increased.

Paradoxically, the mixed and limited statistical support for the effects of resource type dominance on food webs is consistent with the equally confused understanding of the function of terrestrial organic matter in aquatic communities. While data reflecting the assimilation of terrestrial organic matter into aquatic food webs are substantial (Fig. 3; Mitrovic and Baldwin 2016; Jardine et al. 2017), allochthonous plant input is thought to be of limited utility because of its biochemical incompatibility with the nutritional requirements of animal consumers (Brett et al. 2017). Moreover, allochthonous inputs are not inherently equal. For example, plants with C_4 carbon fixation pathways are less biochemically favorable than their C_3 counterparts (Clapcott and Bunn 2003) and are thus unlikely to have a significant influence on food web structure. Potential differences in the bioavailability of allochthonous material is even more drastic when comparing terrestrial plant matter to terrestrial animal prey (e.g., terrestrial insects; Brett et al. 2017; Jardine et al. 2017).

Considering previously documented associations between ecosystem size and food web structure (Post et al. 2000; Sabo et al. 2010), we did not expect low parsimony in candidate SEMs controlling for physical environmental variables (Supporting Information Appendix E). A possible confounder underlying the incongruence is the influence of habitat heterogeneity,

often linked with resource availability (O'Connor 1991). Because larger habitats may support greater heterogeneity, previously observed links between ecosystem size and food web structure could also be a function of resource availability. Across contrasting ecosystems (i.e., temperate lakes and temperate streams (Post et al. 2000; Sabo et al. 2010) vs. tropical lakes in our study), the relative primacy of habitat size/complexity and nutrient level would therefore be contingent on resource type dominance (i.e., relative allochthony discussed above).

The lack of statistical support for the “biotic filtering” hypothesis is not unexpected considering the paucity of published data directly linking community/functional assemblages with food web structure or vice versa (Liew et al. 2016a). In the context of our study, the absence of a clear relationship between functional assemblage and food web properties could also reflect intraspecific phenotypic plasticity (Stauffer and van Snick Gray 2004; Parsons et al. 2016) and facultative diet-switching (McKaye and Marsh 1983) observed in many species of Cichlidae, the most common fish family in our study sites. Flexibility in diet allows cichlids to adopt different feeding strategies in spite of largely identical functional traits (Supporting Information Appendix C). Because phenotypic plasticity and facultative feeding are responses to environmental conditions (Parsons et al. 2016), the fundamental thesis of our study, that environmental filtering is the main driver of food web structure, remains unchanged.

Synthesis and conclusions

In this article, we demonstrated the probable mechanisms of food web assembly. Our study sites were well-suited in

addressing this critical question in ecology because reservoirs represent a novel habitat type often associated with fluxes in community assemblages driven by species turnovers (Liew et al. 2016b). The sites also shared a common pool of potential colonizers of roughly equal propagule pressure/dispersal probabilities because of Singapore's unique geography (i.e., small island with high levels of accessibility). At the same time, environmental conditions were diverse, with riparian matrices ranging from nature reserves to urban centers. These factors facilitated our testing of the relative roles of environmental and biological variables in a manner that is challenging to replicate in disparate habitat types (e.g., a temperate lake vs. a coastal seagrass community; Dunne et al. 2002b).

There are some caveats in interpreting the findings we present in our study. Differences in spatial and temporal scales often confound ecological studies, so it is important for data to be appropriately contextualized. Here, our study was conducted at the community/habitat level and together with data from Bukovinszky et al. (2008), there is evidence for "environmental filtering" in habitat and microhabitat level food webs. The generalizability of the hypothesis to the ecosystem/drainage level, however, requires further research. This is because a simple extrapolation of our findings is unlikely to be accurate, considering that the density of interspecific interactions (e.g., trophic links) may not necessarily scale-up proportionately with resource levels (Byers and Noonberg 2003).

In combination with the current state of knowledge about community assembly, we show that the environment does not only shape species assemblages, but also their interactions (i.e., food web structure). The independence of food web structure from species/functional assemblage means that food webs of a community pair associated with identical environmental conditions are likely to be structurally similar, in spite of differences in species/functional composition (Fig. 5; Supporting Information Appendix G). Our study brings empirical food web studies to a closer alignment with food web theory and this could serve as a basis to predictively model changes in trophic interactions under stress; an important management tool for mitigating anthropogenic species and/or ecosystem function loss.

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Conflict of Interest

None declared.

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