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FOOD WEB STRUCTURE BUT NOT ROBUSTNESS DIFFER BETWEEN RIVERS, LAKES AND ESTUARIES

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Abstract: The pervading physical habitat differences between lakes, rivers, and estuaries should result in structural and thus stability differences in food webs in these three different aquatic habitats. We compared 24 metrics of food web structure and the robustness to loss of both well-connected and random species of 18 well-resolved food webs from six lakes, six rivers, and six estuaries. Robustness measures the proportion of species that need to be removed for 50% of all species to be lost/disconnected. Riverine food webs had lower neighborhood clustering and greater variability in prey vulnerability than estuaries and lakes. Typically, rivers experience physical disturbance relatively more frequently and with greater severity than estuaries and lakes. Disturbance may drive rivers to have lower clustering and have greater proportions of early successional taxa that are mobile and have little armor, and hence greater variability in their vulnerability to predation. Despite the observed differences in food web structure, these did not drive differences in modelled food web robustness between the three habitats. Similarities in robustness may be a result of freshwater organisms having similar body-size ratios between predator and prey/resource taxa thereby driving similar link distributions.

Keywords: allometric scaling; aquatic ecosystem; clustering coefficient; ecological networks; stability.

INTRODUCTION

Global freshwater biodiversity is under considerable threat. In North America alone freshwater ecosystems are experiencing extinction rates five times higher than terrestrial ecosystems (Ricciardi & Rasmussen 1999, Dudgeon *et al.* 2006, Dudgeon 2010, Vorosmarty *et al.* 2010). These declines in biodiversity have resulted from multiple interacting stressors (Matthaei *et al.* 2010, Wagenhoff *et al.* 2011, Piggott *et al.* 2012, Leps *et al.* 2015) including water abstraction for consumptive and agricultural needs (Dewson *et al.* 2007, Poff & Zimmerman 2010, McDowell *et al.* 2011), invasive species (Olden *et al.* 2010, Collier & Grainger 2015), channelization, sedimentation, eutrophication (Carpenter *et al.* 1998, Allan 2004), and changing climate regimes (Palmer *et al.* 2008, Death *et al.* 2015).

Lakes, rivers, and estuaries are all impacted by these stressors, though habitat differences may yield differences in community structure that affect the ability of the community to respond to or resist such disturbances. Lakes are relatively large, deep, standing bodies of water with soft sediment bottoms; communities are typically pelagic and heavily influenced by internal thermal stratification and seasonal mixing (Wetzel 2001). Rivers are flowing bodies of water, with constant mixing, variable flows and typically gravel bottoms; communities are heavily influenced by allochthonous inputs, gravel movement, and flow

(Wetzel 2001). Estuaries represent the inland mixing zone between a river outflow and coastal waters, are usually soft-bottomed and not only experience variable river flows but also semi-diurnal water fluctuations from tidal movement (Wetzel 2001). Estuarine communities are typically a hybrid of the riverine and coastal communities and impacted by continual sediment deposition and disruption.

If the differences between freshwater habitats result in differences in the skewness of the distribution of links and/or change food chain lengths, then differences in topological robustness may arise. Robustness is a measure of food web stability that assesses the capacity of a web to maintain topological structure following species extinction (Dunne *et al.* 2002a, Dunne *et al.* 2005, Donohue *et al.* 2016). Food webs with more dietary links per capita (greater connectance) and a greater abundance of generalist species (networks with uniform degree distributions) are hypothesized to have greater topological robustness to cascading extinctions (Sole & Montoya 2001, Dunne *et al.* 2002a, Ulanowicz *et al.* 2009, Canning & Death 2018). Broad diets allow alternative energy pathways to continue supporting predators should other pathways be perturbed; whereas the rigid and narrow diet of specialists may prevent the compensatory effects of alternative links (Sole & Montoya 2001, Dunne *et al.* 2002a, Ulanowicz *et al.* 2009). Long food chains may also reduce robustness because the loss of basal species will cascade further up the food chain, thereby impacting more species (Freedman & So 1985, Rooney *et al.* 2006, Rooney & McCann 2012, Saint-Béat *et al.* 2015, Canning & Death 2017).

Disturbance can influence both the distribution of links across species (degree distribution) and food chain length. Highly disturbed communities are often observed to be composed largely of generalists with broad diets, while communities in more stable environments tend to have a greater proportion of specialist species (Kitahara *et al.* 2000, Marvier *et al.* 2004, Devictor *et al.* 2008, Canning *et al.* 2018). Therefore, it is plausible that disturbance can affect the composition of generalist/specialist taxa, which can in turn affect the overall food web link (degree) distribution and consequential robustness to species loss (Vázquez & Simberloff 2002, May 2006, Ulanowicz *et al.* 2009). Highly disturbed ecosystems also tend to have shorter food chains and may, therefore, have greater robustness to cascading species extinction (Jenkins *et al.* 1992, Post 2002, McHugh *et al.* 2010, Sabo *et al.* 2010a, Canning *et al.* 2018).

Lakes tend to have more constant environmental conditions than estuaries and rivers as they do not experience large changes in flow regime and sediment/gravel movement from floods or tides (Wetzel 2001). Lake communities tend to be regulated by internal feedbacks and biotic interactions (Scheffer & van Nes 2007), whereas the diversity of river communities is often driven, at least in part, by flood regimes (Resh *et al.* 1988, Death & Winterbourn 1995, Lake 2000, Death 2008). The environmental constancy of lakes may result in low robustness to cascading species extinction by allowing skewed degree distributions and long food chains to occur creating vulnerable hubs. Therefore, lakes may be more susceptible to collapse than riverine and estuarine communities (Briand 1985, Zanden & Fetzer 2007).

Lake food webs also have greater nutrient uptake and retention than estuaries and rivers, and thus provide greater opportunity for communities to take up and utilize nutrients (Saunders & Kalff, 2001). Greater assimilation of a limiting nutrient can permit higher primary productivity, which in turn allows for more energy to flow through the food webs to higher trophic levels, leading to longer food chains (Vander Zanden *et al.* 1999, Marks *et al.* 2000). Furthermore, nutrients are not always assimilated evenly across taxa, which can drive more species consuming the highly-productive taxa, skewing the link distribution and making the web vulnerable to the loss of the well-connected taxa (Ulanowicz 1997, Dunne *et al.* 2002a). Therefore, the larger uptake and retention of nutrients in lakes may result in webs with longer chains, more skewed link distributions and consequently lower robustness than rivers and estuaries (Briand 1985, Zanden & Fetzer 2007).

If we are able to identify and protect the most sensitive freshwater habitats then we may be able reduce or halt the continued decline of freshwater species (Ricciardi & Rasmussen 1999, Dudgeon *et al.* 2006, Dudgeon 2010, Vorosmarty *et al.* 2010). The recent availability of more complete and relatively well-resolved food webs across a range of freshwater ecosystems (Thompson & Townsend 2004, Hechinger *et al.* 2011, Sánchez-Hernández *et al.* 2015) allows for comparisons in food web structure and robustness between freshwater and brackish water habitats. In this study, we test the hypothesis that lake, estuarine and riverine ecosystems differ in food web topology and, as a result, differ in robustness. We predict that river food webs, being the most disturbed, will have the shortest food chains, the most uniform degree distributions and the greatest robustness, whereas lakes will have the longest food chains, most skewed degree distributions and be the least robust; whilst estuaries will have moderate disturbance with robustness intermediate to rivers and lakes.

MATERIAL AND METHODS

We compiled 18 well-resolved (71 – 96% resolved to genus or species level) aquatic food webs (Table 1; Figure 1). To assess resolution, we measured the proportion of taxa identified to species or genus level. Six webs were from estuaries, six from lakes and six from rivers; while there were many river food webs available, most were from similar and nearby rivers to those included in the study, and there were very few lake and estuarine food webs of similar resolution publicly available.

For each food web, Network 3D (Yoon *et al.* 2004, Williams 2010a) was used to calculate 24 metrics of food-web topology including connectance, mean linkage density, trophic level proportions (by species), mean cluster coefficient, as well as measures of food chain length, degree distributions (including generality and vulnerability), nestedness, energy pathway channelization, and redundancy (Table 2).

Food web robustness is defined as the percentage of taxa that need to be removed for 50% of all nodes to become extinct (Dunne *et al.* 2002a). Food web robustness was calculated for each web by sequentially removing taxa using either of two removal sequences: 1) removal of the most connected taxa, or 2) random removal of taxa (averaged from 1000 iterations with replacement each time). Species deletion analysis was also carried out in Network 3D (Yoon *et al.* 2004, Williams 2010a). Secondary extinctions occurred when a species had no available dietary links remaining or when completely disconnected if it was a basal species.

Using Primer 6 (Clarke & Gorley 2006) with PERMANOVA+ (Anderson *et al.* 2008), Non-parametric Multidimensional Scaling (NMDS)

Table 1. The habitat, location, taxonomic richness, connectance, and reference source for 18 freshwater food webs. Resolution is the percentage of taxa nodes identified to species or genus level.

Food web	**Habitat**	**Location**	**Number of taxa**	**Connectance**	**Resolution**	**Citation**
Lake Nyasa	Lake	Tanzania	37	0.055	83.8%	(Fryer 1959)
Bridge Brook	Lake	New York, USA	75	0.098	95.0%	(Havens 1992)
Little Rock	Lake	Wisconsin, USA	181	0.072	93.0%	(Brezonik *et al.* 1986)
Skipworth	Lake	England	35	0.310	91.0%	(Warren 1989)
Cimera	Lake	Spain	79	0.103	85.7%	(Sánchez-Hernández *et al.* 2015)
Grande de Gredos	Lake	Spain	85	0.074	91.8%	(Sánchez-Hernández *et al.* 2015)
Deep Creek	River	Idaho, USA	32	0.137	90.6%	(Koslucher & Minshall 1973)
Bere Stream	River	England	142	0.069	91.5%	(Woodward *et al.* 2008)
River Aire	River	England	60	0.051	83.3%	(Percival & Whitehead 1929)
River Dee	River	Wales	34	0.092	76.5%	(Badcock 1949)
Akatore	River	New Zealand	84	0.032	96.4%	(Thompson & Townsend 2004)
Martins	River	Maine, USA	105	0.031	96.2%	(Thompson & Townsend 2003)

Table 1. Continued on next page…

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Food web	Habitat	Location	Number of taxa	Connectance	Resolution	Citation
Upper Tagus Estuary	Estuary	Portugal	29	0.086	79.3%	(Moreira *et al.* 1992)
Carpinteria Salt Marsh	Estuary	California, USA	272	0.054	71.3%	(Hechinger *et al.* 2011)
Estero de Punta Banda	Estuary	Mexico	355	0.048	63.1%	(Hechinger *et al.* 2011)
Bahía Falsa	Estuary	Mexico	289	0.048	63.3%	(Hechinger *et al.* 2011)
Ythan Estuary	Estuary	Scotland	93	0.049	86.0%	(Milne & Dunnet 1972)
St Marks	Estuary	Florida, USA	51	0.104	71.0%	(Baird *et al.* 1998)

was used to examine the multivariate similarities in food web topology between the three habitat types (Clarke 1993). For this Euclidian dissimilarity distances were used, calculated from all 24 metrics of topology (normalized). One-way Permutational Multivariate Analysis of Variance (PERMANOVA) with 9999 permutations was used to test the difference in overall web topology between the three habitats (Anderson *et al.* 2008).

The differences in each of the food web metrics and robustness score between the three ecosystems was examined using One-way Analysis of Variance (ANOVA) in R 3.0.3 (R Development Core Team 2012). Tukey's Honest Significant Difference post-hoc test was used to examine metrics where ANOVA differences were significant. The Holm's sequential Bonferonni procedure was applied during all multiple comparison significance testing.

Figure 1. The global locations of the 18 aquatic communities studied. Lakes are represented by circles, rivers by squares, and stuaries by triangles. See table 1 for more detail on location and primary references.

Table 2. Mean food web metrics (and their formulae) for six lakes, six estuaries, and six rivers. F-statistics and p-values are from ANOVA's test for differences between habitats. Degrees of freedom are 1 and 16. L is the total number of links; T is the number of top predators; I is the number of intermediate taxa; B is the number of basal taxa; H is the number of herbivores; Can is the number of cannibals; Nloop is the number of species in a closed loop; l is the connection matrix; TPi is the prey-averaged trophic level of species i; TSi is the shortest trophic level of species I; O is the number of species feeding on more than one trophic level; ki is the number of immediately connected taxa (i.e., the number of taxa in the neighbourhood, |ni|; t is the number of triplets with an irreducible gap; T is the total number of triplets possible. A triplet is an irreducible gap with at least three non-monophagous consumers. Vy is the degree of paired nestedness for an individual pair; Gen is number of feeding links each consumer has; Vul is the number of predators each resource taxa has; Deg is the number of links each taxa has; Res is the number of resource taxa; and Cons is the number of consumers.

Metrics	Formulae	Lakes	Estuaries	Rivers	F-stat	p-value
Number of taxonomic groups (node count)	N	82.00	181.50	56.50	0.01	0.92
Mean linkage density	L/N	7.97	9.60	3.41	1.78	0.20
Connectance	L/N^2	0.12	0.06	0.08	2.00	0.18
Fraction of top taxa	T/N	0.10	0.14	0.31	6.71	0.02
Fraction of intermediate taxa	I/N	0.61	0.73	0.36	3.89	0.07
Fraction of basal taxa	H/N	0.29	0.13	0.33	0.12	0.73
Fraction of herbivores	B/N	0.40	0.23	0.39	0.56	0.46
Fraction of cannibals	Can/N	0.10	0.02	0.00	6.34	0.02
Fraction of taxa within loop	Nloop/N	0.09	0.19	0.00	0.95	0.34
Mean short-weight trophic level (Williams & Martinez 2004)	$\sum_{i=1}^{N} \frac{TP_i TS_i}{2N}$	1.97	2.91	1.83	0.03	0.87
Mean shortest chain to a basal species (Williams & Martinez 2004)	$\sum_{i=1}^{N} \frac{TS_i}{N}$	1.88	2.34	1.77	0.02	0.90
Fraction of omnivores (taxa feeding on multiple trophic levels)	O/N	0.39	0.53	0.31	0.10	0.75
Characteristic path length (Williams & Martinez 2004)	$\overline{TP_i}$	2.12	2.20	2.24	0.93	0.35
Mean clustering coefficient	$\frac{1}{N} \sum_{i=1}^{N} \frac{\lvert n_i \rvert}{k_i(k_i - 1)}$	0.19	0.11	0.07	10.07	0.006
Diet Continuity (Cattin *et al.* 2004)	t/T	0.12	0.08	0.32	4.53	0.05
Nestedness based on overlap and decreasing fill (Almeida-Neto *et al.* 2008)	$\frac{\sum V}{N(N-1)}$	0.32	0.21	0.37	0.66	0.43

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Table 2. Mean food web metrics (and their formulae) for six lakes, six estuaries, and six rivers. F-statistics and p-values are from ANOVA's test for differences between habitats. Degrees of freedom are 1 and 16. L is the total number of links; T is the number of top predators; I is the number of intermediate taxa; B is the number of basal taxa; H is the number of herbivores; Can is the number of cannibals; Nloop is the number of species in a closed loop; l is the connection matrix; TPi is the prey-averaged trophic level of species i; TSi is the shortest trophic level of species I; O is the number of species feeding on more than one trophic level; ki is the number of immediately connected taxa (i.e., the number of taxa in the neighbourhood, |ni|; t is the number of triplets with an irreducible gap; T is the total number of triplets possible. A triplet is an irreducible gap with at least three non-monophagous consumers. Vy is the degree of paired nestedness for an individual pair; Gen is number of feeding links each consumer has; Vul is the number of predators each resource taxa has; Deg is the number of links each taxa has; Res is the number of resource taxa; and Cons is the number of consumers.

Standard deviation of consumer restricted generality distribution (Williams 2010b)	SD (Gen)	1.05	1.20	0.74	1.52	0.24
Standard deviation of resource restricted vulnerability distribution (Williams 2010b)	SD(Vul)	0.66	0.74	1.04	10.2	0.006
The standard deviation of the link distribution (Williams 2010b)	SD(Deg)	0.74	0.81	0.78	1.11	0.31
The entropy of the consumer restricted generality distribution (Williams 2010b)	$\sum \frac{Gen}{L} \log \frac{Gen}{L}$	2.14	2.58	2.00	0.02	0.89
The entropy of the resource restricted vulnerability distribution (Williams 2010b)	$\sum \frac{Vul}{L} \log \frac{Vul}{L}$	2.13	2.76	2.00	0.02	0.97
The entropy of the link distribution (Williams 2010b)	$\sum \frac{Deg}{L} \log \frac{Deg}{L}$	2.59	3.27	2.40	0.01	0.91
The percentage of resource taxa	Res/N*100	86.31	86.00	68.98	6.71	0.02
The percentage of consumers	Con/N*100	73.53	86.70	66.56	0.12	0.73

RESULTS

Species richness ranged from 29 to 355, connectance from 0.03 to 0.31, and mean shortest chain length from 1.47 to 2.58 across the 18 webs, though there was no significant difference in species richness, connectance and food chain length between the three habitats (Table 2).

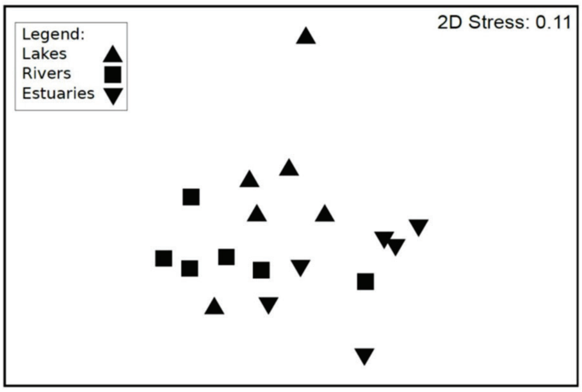

Figure 2. Non-parametric Multidimensional Scaling (NMDS) plot of food web metrics for 18 aquatic communities (stress = 0.11). Lakes are represented by triangles, rivers by squares, and estuaries by inverted triangles. See Table 1 for more detail on locations and primary references.

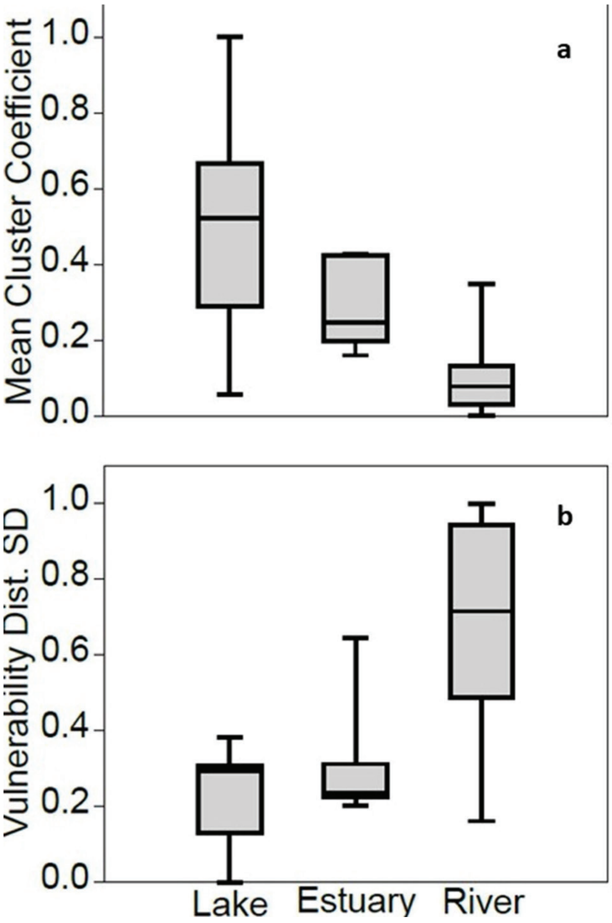

Figure 3. Boxplot of mean cluster coefficient (a) and standard deviation of the normalized vulnerability distribution (b) for 18 aquatic food webs of three different habitats (lakes, estuaries, and rivers).

In an NMDS, river food webs were plotted to the left of axis one and estuaries to the right, with most lakes in the centre (Figure 2). The food webs from the three habitat types differed in their structure although there was some overlap (F = 2.92, p = 0.009).

Of all the metrics assessed, the three habitats only differed significantly in their mean cluster coefficients ($F_{1,16}$ = 10.07, p = 0.006; Figure 3a), and their standard deviation in vulnerability (number of predator) distribution ($F_{1,16}$ = 10.02, p = 0.006; Figure 3b). Rivers had lower mean cluster coefficients than lakes (p = 0.008), and there was no difference between lakes and estuaries (p = 0.09). Rivers had a much larger variation (standard deviation) in vulnerability (number of predator) distribution

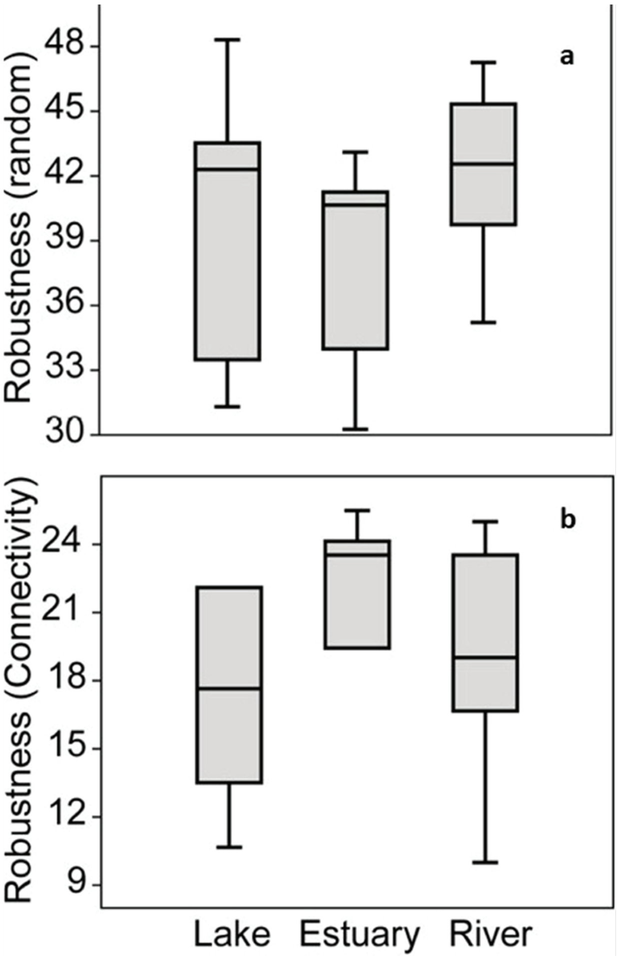

Figure 4. Boxplot of network robustness of 18 aquatic food webs to the loss of random taxa (a) and loss of the most connected taxa (b) depending on their habitat (lakes, estuaries, or rivers). Robustness is the proportion of direct removals required for > 50% of species to be lost.

than lakes (p = 0.006); there was no difference between lakes and estuaries (p = 0.56). The fraction of top taxa was also marginally significantly greater for rivers than estuaries and lakes ($F_{1,16}$ = 6.71, p = 0.02) (Table 2).

Food web robustness did not differ significantly between the three habitats when taxa were removed randomly ($F_{1,16}$ = 0.72, p = 0.50; Figure 4a) or when most connected taxa were preferentially removed ($F_{1,16}$ = 0.15, p = 0.86; Figure 4b).

DISCUSSION

Food web structure differed between the three habitat types. Whilst only three of the 24 food web metrics assessed differed significantly, overall there were also significant differences in food web structure between the three habitats when all 24 metrics were combined in multivariate space. River food webs showed significantly lower node clustering (neighborhood connectivity) than estuaries and lakes. We deem the observed difference in neighborhood connectivity as reliable given that neighborhood connectivity indices showed high robustness to errors in network construction in Fedor & Vasas (2009).

Previous studies have suggested that mean cluster coefficient can be driven by species diversity and connectance (Camacho *et al.* 2002, Dunne *et al.* 2002b, Belgrano *et al.* 2004). However, neither the number of nodes or connectance differed significantly between the three habitats. Species deletion experiments of empirical food webs have consistently shown that clustering decreases with increasing perturbation (Estrada 2007, Navia *et al.* 2012). Furthermore, empirical observations suggest that perturbations impact further than three links away from the initial perturbation (Schoener 1989; Montoya & Sole 2002, Williams *et al.* 2002); therefore, low clustering may be advantageous in webs where species with high neighborhood connectivity are perturbed. Rivers typically face regular and harsh flood disturbances that scour away almost completely all basal taxa and remove substantial portions of invertebrates and fish (Biggs & Close 1989, Death 2008). The flood disturbances that rivers face are likely more deleterious than the cyclic mixing and sedimentation experienced by estuaries and the internal seiches and stratification-mixing regimes in lakes (Wetzel 2001). It is, therefore, plausible that the relatively more severe perturbations of floods in rivers reduce the amount of clustering compared to estuaries and lakes. In general, food webs tend not to have clustering coefficients typical of small-world networks (Watts & Strogatz 1998, Camacho *et al.* 2002, Dunne *et al.* 2002b); our analysis suggests that food webs from lakes may be more similar to small-world networks than food webs from rivers.

Rivers also tend to have greater variability in the vulnerability (number of species consuming prey, or the output links of a node) distribution than estuaries and lakes. The average standard deviation of the vulnerability distribution was approximately four times greater than for lakes and estuaries. Power *et al.* (1996) found that after scouring floods the early successional community consists largely of taxa highly vulnerable to predation, which tended to be mobile and unarmored, or lightly armored, invertebrates, such as mayfly nymphs. Throughout the flood-free period, predator-vulnerable taxa were replaced with less vulnerable taxa that were armored, had silk retreats, or were sessile, thus driving greater variation in prey vulnerability. In lakes and estuaries, however, many of the taxa are sessile and retreat into the benthic sediment (Fuller & Rand 1990, Saha *et al.* 2009). In consequence, high prey vulnerability may drive strong top down control, whereas low prey vulnerability may drive strong bottom up control (Power *et al.* 1992, Atlas & Palen 2014).

We initially hypothesized that the differences in disturbance regimes meant that rivers would have short food chains, whilst lakes would have long food chains and estuaries moderate food chains. However, we did not find support for this hypothesis as we failed to reject the hypothesis that rivers, lakes and estuaries differ in their average food chain length. Food chain length can be determined from a variety of factors other than disturbance, such as thermodynamic constraints, habitat size (both in two and three dimensions) (Post *et al.* 2000, McHugh *et al.* 2010, Sabo *et al.* 2010a, Sabo *et al.* 2010b), resource-consumer body-size ratios (Brose 2010), productivity (Zanden *et al.* 1999, Marks *et al.* 2000), and nutrient enrichment (Townsend *et al.* 1998, Post 2002, Zanden & Fetzer 2007, Warfe *et al.* 2013). It is likely that some of these factors, other than disturbance, are also influencing food chain length in the ecosystems we examined and may explain why we failed to detect significant differences between the habitat types.

The average proportion of species that are top predators differed marginally (after applying the Holms-Bonferroni correction to an alpha of 0.05) between the three habitats. All trophic proportions sum to one; therefore, an increase in one proportion should correspond to a decrease in another. Given that none of the other trophic proportions differed significantly, we consider this likely a false-positive.

Early studies suggested that food webs had an invariant structure regardless of web size or habitat type (Briand & Cohen 1984, Sugihara *et al.* 1989). These findings have been severely criticised for the use of poorly resolved webs, with the current thinking that there is large variation between webs across habitat types (Havens 1992, Bengtsson 1994, Martinez 1994, Petchey *et al.* 2004). Our assessment of these well-resolved webs supports the view that neighbourhood connectivity and vulnerability differ significantly between habitat types (Petchey *et al.* 2004, Zanden & Fetzer 2007).

However, despite the differences in food web structure, robustness did not differ between habitats, irrespective of the sequence of species removal used. This is surprising given that lakes, rivers, and estuaries differ considerably in their disturbance regimes, physical habitat structure, and nutrient dynamics (Wetzel 2001); all of which can potentially alter food chain length and link distributions (both of which can drive food web robustness) (Saint-Béat *et al.* 2015, Mougi & Kondoh 2016). In the webs we examined, neither food chain length nor degree nor generality distributions differed significantly between habitats. Despite the obvious differences in physical structure and disturbance between the three habitats, it may simply be that disturbance has little influence on link distribution and robustness or that the webs face similar levels of disturbance except in different forms. For example, rivers are often disturbed by floods, estuaries by sedimentation and lakes by internal seiches and stratification-mixing regimes (Wetzel, 2001).

Alternatively, recent analysis suggests that allometric scaling may enhance stability (including topological robustness) by altering dietary breadth which can alter connectance and population dynamics (Woodward *et al.* 2005, Brose *et al.* 2006, Brose 2010, Kartascheff *et al.* 2010, Digel *et al.* 2011, Thierry *et al.* 2011, Heckmann *et al.* 2012). The analysis of a large, global database of the body masses of consumers and prey found animals from lakes and streams to have very similar body size ratios compared to marine and terrestrial ecosystems (Brose *et al.* 2006b). Therefore, the similarities in body sizes of predators relative to their prey may translate to the similarities in link distribution and robustness observed. Instead, the differences between lakes, rivers, and estuaries arose in terms of neighbourhood connectivity and vulnerability distributions, which both can affect topological robustness (Rooney & McCann 2012, Saint-Béat *et al.* 2015, Mougi & Kondoh 2016).

While we did not detect any differences in robustness, this does not mean that there are no differences in community stability between the three ecosystems. Robustness, resilience, resistance, invasibility, and persistence all contribute to overall community stability (Saint-Béat *et al.* 2015). Therefore, even if robustness does not differ, other aspects of stability may still do. We also only measured web robustness to the loss of both randomly selected and well-connected species loss, hence robustness may still differ under different deletion sequences. An aspect not considered by our analysis is the ability of predators to alter their diet by switching prey (diet plasticity). This study assumes that all potential dietary links were accounted for during the assembly of each web, though there is a reasonable probability that not all links were. Taxa that can easily switch their diets would add to the overall robustness, whilst highly specialised taxa would be deleterious to overall robustness. Furthermore, our assessment of topological robustness assumes webs are bottom up controlled and ignores energetic dynamics, which may mask the effects on trophic cascades of neighbourhood connectivity and vulnerability variation. As explained above, the differences in vulnerability may affect the direction of trophic control which can, in turn, drive differences in stability and other emergent properties such as mutualism and synergism (Ives & Cardinale 2004, O'Gorman *et al.* 2010).

In summary, rivers have lower neighbourhood connectivity and greater variability in the vulnerability of predators than lakes and estuaries.

These differences, however, did not translate into differences in topological robustness to cascading species extinction when species were removed randomly or by their connectivity. Freshwater and brackish water ecosystems typically have similar predator-to-prey body-size ratios which may, in turn, have driven the observed similarities in link distribution and robustness between lakes, rivers, and estuaries (Brose *et al.* 2006b).

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