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The impact of intraspecific variation on food web structure

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Abstract. Accounting for the variation that occurs within species in food webs can theoretically result in significant changes in both network structure and dynamics. However, there has been little work exploring their role with empirical data. In particular, the variation associated with species' life cycles, which is prevalent and represents both trait variation and taxonomic identity, has received little attention. Here, we characterize the structural consequences of life stage variation in five food webs, including a newly compiled web from the Arabian Gulf. We show that making life stage variation explicit in food webs results in larger food webs that possess consistent structural changes that are separate from the changes in structure that come simply from increasing the number of nodes in the webs. Furthermore, we show that the magnitude of these changes is related to ontogenetic specialism, the degree of overlap in the ecological niches of life stages. These results demonstrate the capacity of intraspecific variation to affect ecological networks and indicate the potential usefulness of stage-structured food webs, which capture size and taxonomic information, to represent variation below the species level.

Key words: ecological network; empirical food web; ontogenetic niche shift; ontogeny; predator–prey; stage structure.

Introduction

Ecological network research provides a powerful framework with which to study the structure and dynamics of communities. It has been used successfully to explore a number of topics in ecology such as the sensitivity of communities to species loss (Dunne et al. 2002a, Ebenman and Jonsson 2005, Gilljam et al. 2015), the factors driving the observed similarities in their structure (Dunne et al. 2002b, Dunne 2006) and the relationships between community dynamics and functioning (Thompson et al. 2012, Schneider et al. 2016). Despite these successes, the study of ecological networks has attracted considerable criticism due to the simplistic taxonomic representation of communities that are commonly used (Gilljam et al. 2011, Poisot et al. 2015a). In particular, the tendency of ecological network studies to treat species as homogenous units has been called into question, as it ignores the intraspecific variation inherent in natural populations (Post et al. 2008, Woodward et al. 2010, Bolnick et al. 2011, Gilljam et al. 2011, Violle et al. 2012). Individuals within the same species vary in their size, morphology, behavior, and physiology (Bolnick et al. 2002, Woodward et al. 2010). Such variation can result in differences in the ecological interactions that individuals of a given species are part of, which in turn may scale up to community-wide changes in ecological network structure and dynamics (Woodward et al. 2010, Bolnick et al. 2011, Gilljam et al. 2011, Kuppler et al. 2017).

A growing body of theoretical work (Barbour et al. 2016, Gilljam 2016, Zee and Schreiber 2017) documents the changes that this intraspecific variation can make to ecological networks, but empirical data on the topic are still relatively poor (Woodward et al. 2010, Gilljam et al. 2011). In particular, there has been little work identifying the structural network consequences of intraspecific variation that arises as a result of organisms moving through their life cycle, life stage variation, despite its prevalence in nature (Preston et al. 2014).

The potential for life stage variation to impact food web structure is driven by the concept of the ontogenetic shift, the change in the ecological niches that individuals occupy over their lifetime (Werner and Gilliam 1984). It is estimated that ~80% of all animal taxa undergo some form of ontogenetic shift (Werner 1988, Woodward and Hildrew 2002), which are commonly linked to changes in diet. They thus alter the interactions that an individual takes part in throughout a community, potentially affecting network structure. The intensity of these changes can vary greatly, ranging from species that are complete ontogenetic specialists, having unique sets of ecological interactions at each life stage, to those that are ontogenetic generalists, whose ecological interactions remain the same across their lives (Rudolf and Lafferty 2011).

The few studies that have considered the effects of this variation among life stages tend to focus on body size as the sole determinant of interactions across life stages (Woodward et al. 2010, Gilljam et al. 2011). Though size has been demonstrated to be a good predictor of species interactions, this approach fails to account for other traits that will change across species lifetimes and that may be important in determining network structure (Eklöf et al. 2013). Alternatively, life stage variation, which captures ontogeny, can be accounted for by representing individual life stages as their own nodes with unique sets of links, allowing traits beyond body size to be represented. This approach was used by

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Rudolf and Lafferty (2011) who showed that this variation reduced food web robustness (i.e., the capacity of species loss to cause further extinctions based purely on network topology). However, there has been no work exploring the impact on network structure of individual variation defined by life stage (ontogeny).

Here, we assess the effects of including life stage information on several attributes of food web network structure and explore the role of ontogenetic shifts and specialism as a driver in these changes. We take a similar approach to Dunne et al. (2013) who looked at the structural consequences of including parasite species using a number of food web metrics. Central to this approach is the question of whether including these additional nodes (life stages in our case) alters network structure beyond the expected effects of simply adding more links and nodes to the food web network.

We explore five aquatic food webs for which there is resolution of life stages, including a new and very large food web from the Arabian Gulf. We specifically compare the network structure of versions of the webs with life stage information (ontogenetic resolution) to versions without the life stage information (taxonomic) by distinguishing between the structural changes that occur as a result of changing diversity and complexity (i.e., changing the size and connectedness of the networks) and the effects of including life stage structure itself.

Our analyses reveal that the disaggregation of species into their respective life stages has effects that differ from the simple addition of new taxonomic species for both diversity–complexity relationships and several structural metrics. We show that this change is underpinned by how life stage information alters the distribution and arrangement of trophic links throughout the webs and that consistent patterns are seen in the change in network structure across the webs we consider. These findings reinforce the growing consensus in network ecology of the importance of intraspecific variation. Our results suggest that an approach centered on life stages/life cycles may provide a way to account for the complexities that arise from considering intraspecific variation while retaining detail on the taxonomic identity of the species involved, which remains important in conservation management.

Methods

Data

We analyzed five highly resolved aquatic food webs with a substantial amount of life stage information including a newly compiled food web from the Arabian Gulf, which is described below (Ali 2015). Three of the other four food webs were compiled from estuaries across the North American Pacific coast: Carpinteria Salt Marsh, California (CSM); Estero de Punta Banda, Baja California (EPB); and Bahía Falsa in Bahía San Quintín, Baja California (BSQ) (Hechinger et al. 2011) with the other being from a pond ecosystem in Northern California, Quickpond (Preston et al. 2012).

In these food webs, each species that is disaggregated into life stage is represented by an individual node with its own trophic links to other species/life stages. Because of this, we were able to generate a second version of each of the webs in order to assess the effects of including this life stage information. This second, non-life-stage version was obtained by aggregating all of a species' life stages and trophic links, creating a single node with links to all the species that each life stage was connected to.

In addition to calculating the proportion of species in each web with life stage information, we determined the average degree of ontogenetic specialism using the method detailed by Rudolf and Lafferty (2011), calculating the similarity of the sets of resources and consumers across each species' life stages using the Jaccard index and averaging these values across the webs. This results in single values for prey and predator specialty in each web that range from 1, where every life stage has identical interactions, to 0, where all life stages have unique trophic links.

In addition to the five webs with life history information, a further six from a range of aquatic environments were used for comparison of diversity–complexity relationships of the life stage webs. The webs, in order of size, were (1) Benguela, a web characterizing the fisheries and marine mammals of the coast of South Africa (Yodzis 1998); (2) Chesapeake Bay, a community from an estuary in the northeast United States (Baird and Ulanowicz 1989); (3) Ythan Estuary, an estuarine community from northeast Scotland (Hall and Raffaelli 1991); (4) Barents, a community from the Barents Sea in the Arctic Ocean (Planque et al. 2014); (5) Jamaica, one of three food webs from a coral reef community in the Caribbean (Roopnarine and Hertog 2012); (6) Weddell Sea; the marine community of the Weddell Sea (Jacob et al. 2011).

The Arabian Gulf food web

The newly described Arabian Gulf food web characterizes the marine community found within the Arabian Gulf (also known as the Persian Gulf) consisting of the commercially important fish and invertebrates in the area as well as various other species. The web is, to our knowledge, one of the largest food web ever constructed with 918 nodes representing species and their various life stages and 58,225 trophic links. Detailed metadata for species and their life stages was collected including their taxonomy, length, commercial importance, and the life stage they represent. Data for the food web were obtained from literature and expert opinion from the Kuwait Institute of Scientific Research and then verified using the World Register of Marine Species with the worrms package from ROpenSci (Chamberlain 2017, Horton et al. 2017). Though most evidence was obtained from studies of the Arabian Gulf itself, some data were obtained from studies in the wider Indian Ocean of which the Arabian Gulf is part of and with which it shares many species (Ali 2015).

Analyses

We assessed the structural differences between the versions of the food webs both with and without life stages by analyzing four aspects of food web structure: (1) the diversity–complexity relationship, (2) six structural metrics, (3) the network degree distributions, and (4) motif expression.

All assessments of structure focused on comparing each of the taxonomic and life stage webs to a null model where the size of the web (number of nodes/species) simply increases. This allowed us, for all four of the structure evaluations, to challenge the hypothesis that life stage webs generate structural change above and beyond simply adding more species to the community.

Analyses were carried out using R (R Core Team 2016) with the cheddar and iGraph packages (Csardi and Nepusz 2006, Hudson et al. 2013) along with the Network3D software (Yoon et al. 2004, Williams 2010a). All food web data and analysis scripts based in R are available online (see *Data Availability*).

Diversity–complexity relationships

Diversity–complexity relationships have long been an area of interest in food web ecology, describing how the complexity of networks (the number of links) responds to changes in their size (the number of nodes). Previous work has found that this relationship can generally be characterized using a power law relationship with the form $L = a \times S^b$ where L is the number of links a is a constant and S the number of nodes with the value of b ranging between 1.5 and 2.0 (Dunne 2006). We determined the nature of this relationship across our five webs with life stage information and the six from other aquatic environments by using log(L) and log(S) in a regression, allowing us to predict how the number of links in each food web should change as new nodes are added and the size of the webs increases.

We then compared the changes in the number of links that occurred when we included life stage information to that predicted by the power law relationship. This allowed us to determine if the addition of life stages was having an effect beyond that expected with the addition of new species nodes. In order to determine the magnitude of these differences, we used the ratio of the change in the number of links over the change in the number of nodes. If the addition of new life stages is equivalent to the addition of new species nodes, this ratio should be close or equal to the value of b (power law exponent). We then compared the magnitudes of these differences to the degree ontogenetic specialty in each web by calculating Pearson's correlation coefficient.

Structural metrics

We examined the influence of life stage information on six structural metrics tied to the arrangement of links and nodes within each web: the fraction of basal nodes, the fraction of intermediate nodes, the fraction of top-level nodes, the average trophic generality, the average vulnerability, and their respective standard deviations (Table 1). These were all calculated for both versions of each web, with and without life stage information.

The values of these metrics are influenced by the size of the food web considered. We therefore distinguished between the effects of adding new nodes and links from the disaggregation of species into their life stages (Dunne et al. 2013). We compared the values from the taxonomic and life stage version of the five webs with values predicted by webs simulated from the niche model of the same size and connectance (i.e., the proportion of possible links realized in the web).

TABLE 1. Food web metrics.

Metric	Full name	Definition
Bas	fraction basal	the fraction of nodes that have no resources
Int	fraction intermediate	the fraction of nodes that have resources and consumers
Top	fraction top	the fraction of nodes that have no consumers
Gen	trophic generality	the average number of predators per node, normalized by L/S
GenSD	trophic generality standard deviation	the standard deviation of the trophic generality
Vul	trophic vulnerability	the average number of prey per node, normalized by L/S
VulSD	trophic vulnerability standard deviation	the standard deviation of the trophic vulnerability

Notes: Further details can be found in the Structural metrics section, and in Williams and Martinez (2000). L, number of links; S, number of species.

The niche model is a model capable of generating realistic food web structures and has been shown to be accurate in predicting key structural metrics of food webs, making it suitable for comparison with the empirical data (Williams and Martinez 2000). We generated 1,000 webs using the niche model for each version of the webs and calculated the structural metrics detailed above. If life stage variation generates unique changes to food web structure, their statistics will be substantially different from those generated by the simulated niche model in contrast to the taxonomic webs and the simulated niche model webs, which should be more similar.

In order to quantify the difference between the real values and the predictions of the niche model, we calculated the model error (ME). This is given by the difference between the observed value and the median of the model-generated values, normalized by the difference between the median and the 5th or 95th percentile (depending on the direction of the model distribution tail; Williams and Martinez 2008). When $\text{ME} > |1|$ there is a significant difference in the predictions of the model and the observed values. If the niche model is able to predict the values for the webs without life stage information but unable to in webs with life stages, it indicates that the changes in the metric values differ from our expectations when adding new species (i.e., increasing the network size).

Degree distributions

Degree distributions are probability distributions of the numbers of resource or consumer links for each node across a food web. Typically, food webs follow similar patterns of degree distribution with most nodes having few links and few nodes having many links. They offer additional insight into the arrangement of trophic links in the network (Montoya and Sole 2003, Dunne 2009, Dunne et al. 2013). As above, we used a null model to compare the differences in the degree distributions of the life stage and non-life-stage webs.

We generated degree distributions for both resource and consumer node degrees in each version of the five webs, normalizing the counts by the average number of links per node (L/S). We then tested the fit of the MaxEnt model to each these distributions, which generates the least biased probability distribution given a set of data by maximizing entropy while conforming to some given constraint (Williams 2010b). We constrained these distributions by the numbers of nodes and links in each web, as well as the numbers of basal nodes for resource distributions and the numbers of top-level nodes for consumer distributions. We then calculated the goodness of fit, f_G, and the relative width of these degree distributions, W_{95}. An $f_G \leq 0.95$ indicates that an empirical web's distribution does not significantly differ from that of the model at the 95% confidence interval. Values of $-1 \leq W_{95} \leq 1$ indicate that the width of the empirical degree distribution is neither wider ($W_{95} > 1$) nor narrower ($W_{95} < -1$) than the model. By comparing between the fit of the MaxEnt model for each version of the webs (with and without life stages), we can assess how/whether the degree distributions change while accounting for changes in diversity and complexity.

Motif analysis

Motifs are defined as three-node triplet patterns in the web (e.g., trophic change, omnivory, etc.) and can be classified it into 13 possible unique arrangements or "motifs" (Milo et al. 2002). The distribution of these motifs gives information on the patterns of trophic interactions within communities, with consistent patterns of expression having been found across a range of food webs (Stouffer et al. 2007).

We conducted a motif analysis to determine the effects of including life history on the arrangement of trophic links across the webs. In order to assess the differences in motif representation between the life stage and non-life-stage versions of each web, we compared the expression of the 13 motifs in each web to the expression in 1,000 randomly generated food webs, created by randomly assigning links between nodes, maintaining the same numbers of single, double and cannibalistic links as in the original webs. The expression of the 13 motifs relative in the taxonomic or life stage web to the randomly generated webs were calculated using the z score

$$z_i = \frac{\mathrm{N}_{\mathrm{real}} - \langle \mathrm{N}_{\mathrm{rand}} \rangle}{\sigma \mathrm{N}_{\mathrm{rand}}} \tag{1}$$

where $\langle \mathrm{N}_{\mathrm{rand}} \rangle$ and $\sigma \mathrm{N}_{\mathrm{rand}}$ are the average and standard deviation of the numbers of each motifs in the random webs, respectively, giving a vector of 13 z scores (Milo et al. 2002, Stouffer et al. 2007).

In order to compare the z scores of the life stage and non-life-stage webs, we used the uncentered correlation coefficient and ratio of the z score norms (Stouffer et al. 2007). The uncentered correlation coefficient (r) measures the similarity of the direction of motif expression in two given webs (i.e., the tendency of two webs to over and under express the same motifs). Values of r equaling 1 or -1 indicate that the two webs express motifs in similar or opposite directions, respectively, and values closer to 0 indicate there is little similarity. The ratio of z score norms (d) measures the similarity of the magnitudes of motif expression in two webs. We measured this ratio relative to the versions of the webs without life stages meaning that when $d > 1$ the version with life stages had greater magnitudes of motif expression and when $d < 1$ the non-life-stage version has greater magnitudes of expression. Values close to 1 indicate little difference in magnitudes.

RESULTS

Data

The five food webs that contained life stage information varied greatly in the proportion of species with more than one life stage and in the degree of ontogenetic specialism (Table 2). The Arabian Gulf web had the lowest proportion of species with life stage information but exhibited the highest degree of ontogenetic specialty of any of the webs. BSQ, CSM, and EPB webs followed in terms of the proportion of the web with life stage information but were the webs with the lowest degrees of ontogenetic specialty. Quickpond had the highest proportion of the web with life stage information and an intermediate amount of ontogenetic specialty.

Diversity–complexity relationships

A power law was found to accurately describe the diversity–complexity relationship between all five webs with life stage information and the additional six webs ($L = S^b$) with $b \approx 1.73$ (Fig. 1A). This b value falls within the previously reported values, which range between 1.5 and 2.0 (Dunne 2006). The observed increase in the number of links when including life stage information was found to be lower than expected by the power law across all webs with the magnitude of this difference varying between the webs. The magnitude of this difference was also found to significantly correlate with the degree of ontogenetic specialism across all five webs for both species resources and consumers (Fig. 1B).

Structural statistics

For the five webs with life stage information, the niche model correctly predicted ~51% of the metrics (23/35) for the taxonomic versions (without life stages), but only ~43% correctly (15/35) for the life stage version. The numbers of webs for which significant differences were observed between the life stage and non-life-stage versions varied by statistic as did the directionality of these differences. The fraction of basal (Bas) and intermediate nodes (Int) were significantly different in their values for four and three webs, respectively. Both did not vary in the Arabian Gulf and Int did not vary in BSQ. Bas was higher and Int lower when life stages were included. The fraction of top-level nodes (Top) was only significantly different in the BSQ web where it was found to be higher in the life stage version. Both the trophic generality (Gen) and vulnerability (Vun) were not significantly different in the two versions of any of the webs. The standard deviation of trophic generality (GenSD) was higher for BSQ, CSM, and Quickpond.

TABLE 2. Life stage statistics.

Food web	S	L	L/S	C	Bas	Int	Top	Mean TL (prey averaged)	Proportion of web with life stages	Average ontogenetic specialism
Arabian Gulf										
Life stage	918	58,225	63.43	0.07	0.17	0.80	0.02	2.52	0.09	0.45 (0.33)
Taxonomic	635	37,510	59.07	0.09	0.20	0.79	0.01	2.50	–	–
BSQ										
Life stage	290	3,997	13.78	0.05	0.19	0.67	0.13	3.74	0.35	0.02 (0.13)
Taxonomic	172	3,721	21.63	0.13	0.10	0.88	0.01	5.05	–	–
CSM										
Life stage	273	3,971	14.55	0.05	0.15	0.79	0.05	4.00	0.32	0.05 (0.19)
Taxonomic	166	3,709	22.34	0.14	0.07	0.89	0.03	7.84	–	–
EPB										
Life stage	356	5,998	16.85	0.05	0.16	0.80	0.04	3.69	0.36	0.02 (0.11)
Taxonomic	215	5,654	26.30	0.12	0.07	0.92	0.01	6.76	–	–
Quickpond										
Life stage	113	1,905	16.86	0.15	0.19	0.80	0.01	3.40	0.51	0.27 (0.42)
Taxonomic	63	1,088	17.27	0.27	0.08	0.92	0.0	9.83	–	–

Notes: For each web, we report details on the life stage and taxonomic version. S, species richness; L, number of links; L/S = links/species; $C = L/S2$ = connectance; Bas, fraction basal species; Int, fraction intermediate species; Top, fraction top species; Mean TL, mean trophic length. More details can be found in Table 1, the Structural metrics section, and Williams and Martinez (2000). Proportion of web with life stages identifies the proportion of species with life stage information. Average ontogenetic specialism is calculated for the life stage webs following Rudolf and Lafferty (2011) as the similarity of the sets of resources and consumers across each species life stages, using the Jaccard index, and averaging these values across the webs (SD is provided in parentheses). The dashes indicate taxonomic webs, for which these metrics are not calculated. See *Methods: Data* for site codes.

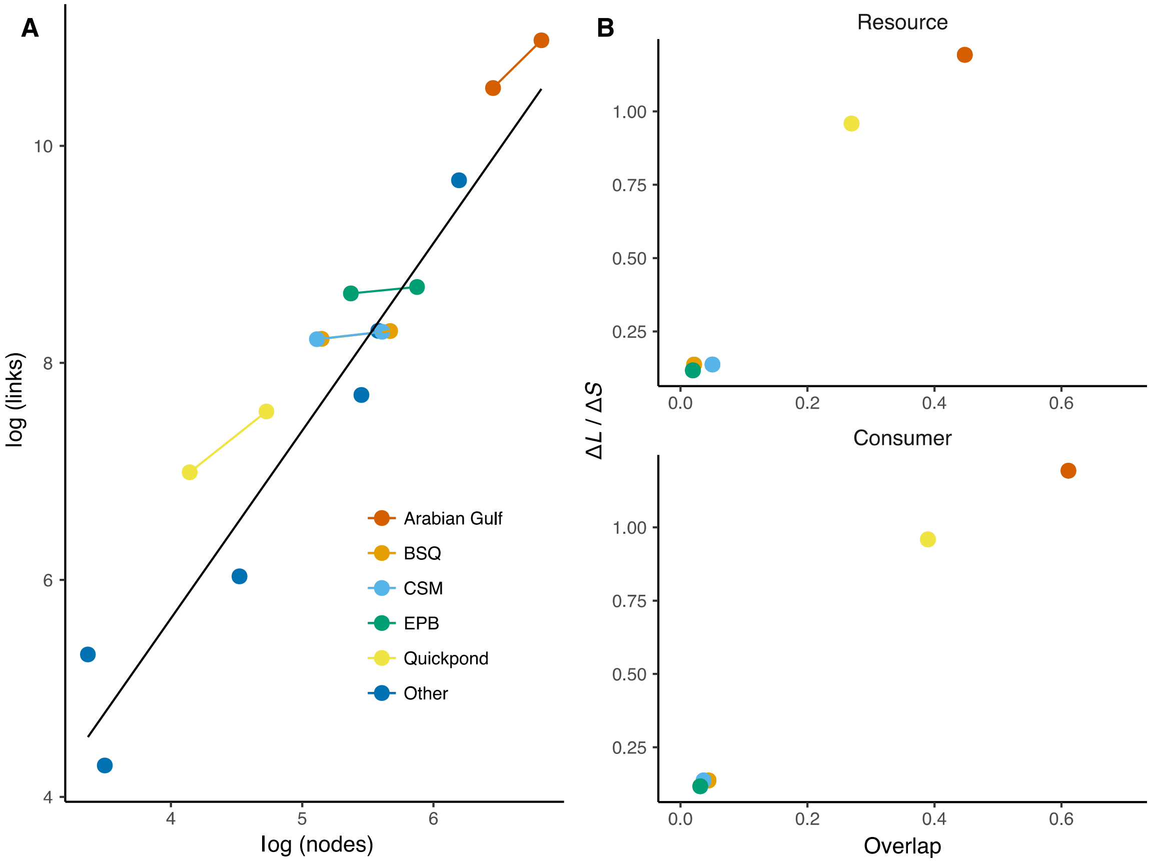

FIG. 1. (A) Diversity–complexity relationship across the five webs with life stage information (multiple colors) and the additional six webs (in blue). The solid black line is fitted from a linear regression across all 11 webs together ($y = 1.73x - 1.27$, $F = 150$, df = 1,9, $P < 0.01$) and shows the overall diversity–complexity relationship from which we predict the changes in the life stage webs. Each point represents a food web with lines being drawn between the webs with and without life stage information to aid visual comparison. (B) The relationship between the relative change in links and nodes (i.e., $\Delta L/\Delta S$) and the average degree of resource and consumer overlap across each of the five webs. Significant correlations were observed for both the resource ($r = 0.98$, $P < 0.01$, $n = 5$) and consumer ($r = 0.99$, $P < 0.01$, $n = 5$) overlap (Pearson's correlation coefficient). See *Methods: Data* for site codes.

Degree distributions

The MaxEnt model was equal in its ability to fit the distributions across all five webs. For both versions of each of the empirical webs, the values of f_G were >0.95 indicating that the empirical distributions were significantly different to those predicted by the MaxEnt models.

However, W_{95} was between -1 and 1 for all comparisons indicating that the width was not significantly narrower or wider in any of the degree distributions as compared to those generated by the MaxEnt models. Degree distributions were thus indistinguishable between taxonomic and life stage webs.

Motif analysis

Motif expression in webs relative to null models followed similar patterns in directionality across the five food webs, though there was a greater degree of variation for some motifs (Fig. 2). All webs under expressed motifs S3, D3, D4, and D8 and displayed no difference in expression for motifs S1, S4, and S5. Motifs S2, D1, D2, D5, D6, and D7 showed a more varied response with no clear over or under expression.

The food webs also showed differences in the expression of motifs by the life stage and non-life-stage versions of each web. The z scores revealed that all the non-life-stage webs

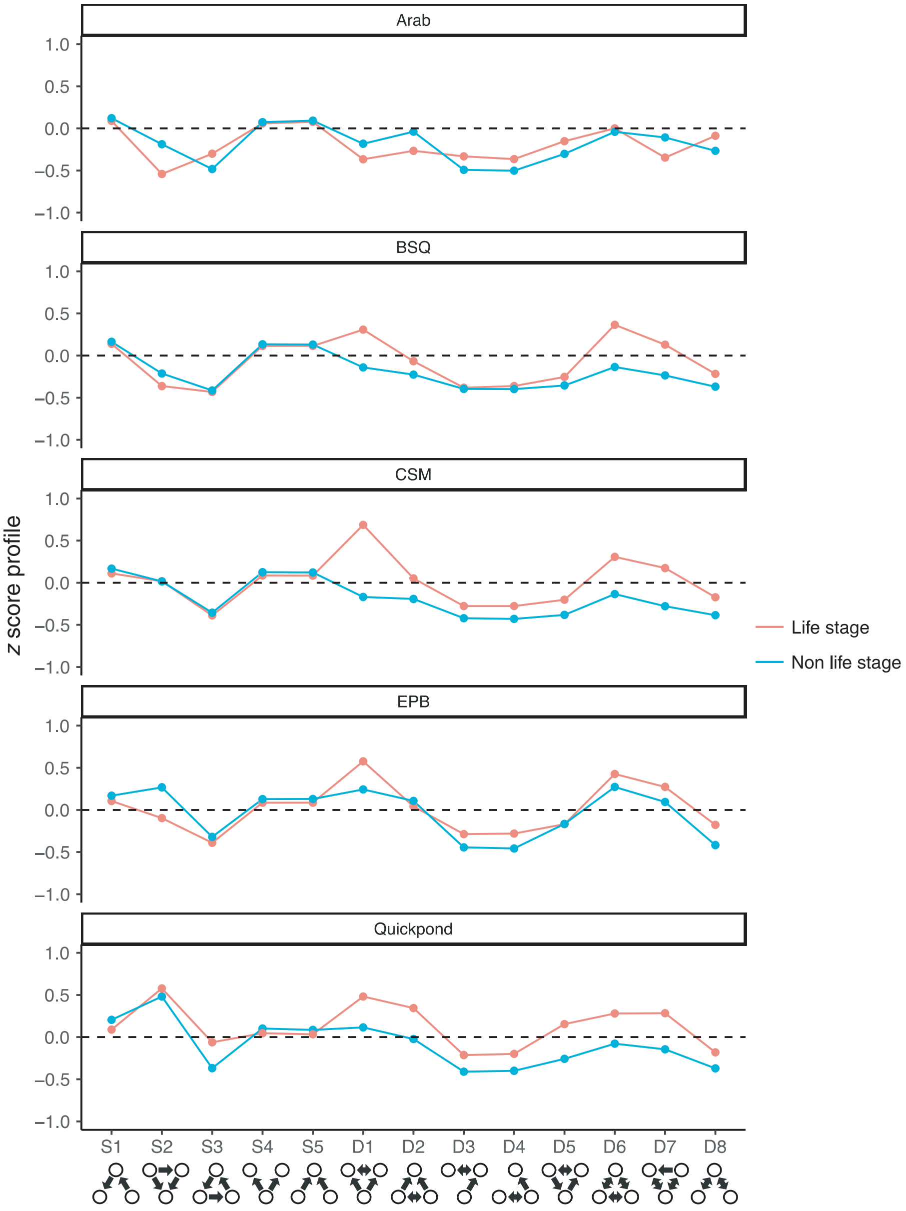

FIG. 2. Motif expression of the five webs with and without life stage information. To facilitate visual comparison of the motif expression, we plot the normalized profile $P_i = z_i/\sqrt{\sum_j z_i^2}$, which is the vector of z scores, normalized to 1 (Milo et al. 2002, Stouffer et al. 2007). Each line represents a single version of a web with color representing the presence or absence life stages. The motifs are shown along the x-axis along with diagrams showing their structure. See *Methods: Data* for site codes.

showed reduced expression of the D3, D4, and D5 motifs relative to the life stage versions and all except the Arabian gulf showed reduced expression of D1, D6, D7, and D8. Little to no difference in motif expression was observed for S1, S3, S4, and S5 across all the webs, and there were no clear patterns of motif expression for S2 and D2.

The webs tended to express motifs with the same directionality in both their life stage and non-life-stage versions as evidenced by their uncentered correlation coefficients for which all were $r > 0$. CSM had the smallest uncentered correlation coefficient (i.e., the least similar directionality of motif expression) with 0.34 followed by Quickpond with 0.51, BSQ with 0.67, EPB with 0.79, and the Arabian Gulf web with 0.78.

The magnitudes of motif expression were larger in the non-life-stage versions of the five webs as shown by their ratios of z score norms, which were all <1. EPB had the ratio of z score norms furthest from 1 (i.e., the least similar magnitude of motif expression) with 0.32 followed by CSM with 0.35, BSQ with 0.40, Quickpond with 0.43, and the Arabian Gulf with 0.68.

Discussion

Intraspecific variation is increasingly recognized as an important factor in the study of ecological networks, with several recent studies demonstrating its potential in influencing network structure (Woodward et al. 2010, Gilljam et al. 2011, Barbour et al. 2016, Kuppler et al. 2017). Despite this, no work has directly addressed how the variation that exists across an individual's ontogeny (e.g., its life stages) affect structure, despite its ubiquity and potential importance in influencing network structure (Werner and Gilliam 1984, Rudolf and Lafferty 2011).

Here, we explore the structural consequences of including life stage information by specifically comparing taxonomic and life stage versions of webs to random webs where nodes are simply added randomly. Our approach formally tests the hypothesis that life stage variation, which captures complexities of ontogeny, has a fundamentally different effect on food web structure than simply adding more species.

Our data and analyses of four classic measures of food web structure reveal that the inclusion of life stages results in consistent changes in network structure that are separate to changes in diversity and complexity, instead resulting from the unique contribution of including life stages themselves. This consistency indicates a possible generality to these effects and a way to capture life stage trait variation. Although our study considers a relatively small sample of networks from only aquatic environments, the prevalence of ontogenetic shifts throughout the animal kingdom means that these changes may be applicable across a wider range of ecosystems (Werner 1988, Polis 1991).

We observed three main structural changes across the food webs we considered. First, the deviation of our food webs from the expectations of the diversity–complexity relationship indicates that the addition of life stages in food webs has effects beyond the simple addition of new species. Life stage webs tended to have fewer links than expected by the power law relationship with the magnitude of the divergence from the predictions being positively correlated with the degree of ontogenetic specialty in the web.

We suggest that there is a certain logic to this. In the case of an ontogenetic specialist, the disaggregation of a species into its life stages will result in the addition of new nodes, each with fewer links than the original species. The opposite is true for ontogenetic generalists where the disaggregation results in the addition of nodes that have similar numbers of links to the aggregated species node. Thus, the combination of these processes means that in webs with more specialism, we see nodes being added with fewer links than would be expected from a species level node. Interestingly this result is in contrast to Dunne et al. (2013), who showed that the addition of parasites did not result in deviation from the expected diversity–complexity relationships.

Second, we saw clear changes in network structural statistics, particularly an increase in the fraction of basal nodes and a decrease in the fraction of intermediate nodes, in webs with life stage information. This change is explained by the life cycle of many aquatic organisms, which often have non-feeding egg or larval stages (Strathmann 1985). When disaggregated to life stage, species that were intermediate can be split into several nodes, one or more of which may be basal. This results in an overall increase in the fraction of basal nodes and a decrease in the fraction of intermediate nodes.

Last, we observed changes in the distribution of network motifs, driven by increased expression of the motifs containing double links in the life stage webs. While we might expect that aggregation would result in more mutual predation (i.e., links of species who both feed and are fed upon by another species across their lives are combined into a single double link), it is important to remember that the z score metric used here represents the expression relative to the null model. This means that the increased expression does not necessarily mean there was an increase in the number of double link motifs but an increase relative to the null expectations of increasing the size of the web.

This increase in expression of double links is hard to interpret biologically. Although the potential importance of double link motifs (i.e., mutual predation) has been identified in previous work (Stouffer et al. 2007), there has been little research on their empirical impacts on the structure and dynamics of ecological networks (Borrelli 2005, Stouffer et al. 2007) suggesting that the causes and consequences of these motifs should be explored further (Klaise and Johnson 2017).

Interestingly, the MaxEnt model was unable to capture the degree distributions of either version of the webs. It was thus impossible to conclude that there is a difference in the degree distributions of each version of the webs. Previous work using the MaxEnt model has interpreted deviations from the predictions of the MaxEnt model as evidence of other ecological or sampling effects affecting the degree distributions (Williams 2010*b*). Given the commonalities between our five webs, it is plausible that this is the case and that other factors are driving their degree distributions that are not accounted for by the MaxEnt model.

Though the structural changes detailed above were observed across most of the webs we analyzed, the Arabian Gulf web often did not express the same changes. This may be due to the lower proportion of species with life stage information compared to the other webs, which would likely reduce the effects of disaggregation. The large size of the web may also have contributed to our inability to detect the same changes as many of the metrics we used have been shown to be scale dependent. Both the niche model (which we used to standardize the differences in our structural metrics), and the expression of motifs in food webs depend on the size of the web that they consider and as such may have prevented us from detecting the actual structural changes (Stouffer et al. 2007, Williams and Martinez 2008, Dunne et al. 2013). This problem will likely be encountered more in the future as improvements in the methods used to compile networks such as metabarcoding and the creation of online databases increase the size of the networks that ecologists have access to, making the development of new techniques a priority for future research (Smith et al. 2011, Clare 2014, Poisot et al. 2015*b*).

We believe that our study has strong implications for work aiming to include intraspecific size variation in food web networks. Size-structure-based research typically attempts to account for both the taxonomic identity of species and the distribution of their body sizes, using these jointly to determine whether interactions occur (Hartvig et al. 2011, Blanchard et al. 2014, 2017). This method has been used to address the role of ontogenetic shifts in marine systems by using size as a proxy for ontogeny. However, this approach fails to take into account the changes in interactions that occur over an organism's life cycle, which we show here can have significant structural implications independent of food web size. The purely stage-structured approach we use here may provide a way for size-structure-based research to include the non-size-based effects of ontogeny that are captured in the changing interactions of individual life stages.

Our findings show that the inclusion of life stages in food webs has significant effects on network structure, changing the distribution of nodes and links throughout webs as well as the patterns of their arrangement. The conceptual accessibility of ontogeny, the evidence that the distribution of ontogenetic specialism is critical and the capacity to isolate impacts of life stage variation from changes to diversity and complexity suggest a robust tool to account for role of intraspecific variation on food web structure.

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DATA AVAILABILITY

Data and scripts are available on GitHub: https://doi.org/10.5281/zenodo.1408967.