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Inferred seasonal interaction rewiring of a freshwater stream fish network

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Despite evidence that seasonal variation may lead to the persistence of competing species, studies on the effect of seasonality on community network structures are sparse. Identifying whether seasonal network changes are the result of turnover or rewiring (i.e. rearrangement of interactions among species), also remains understudied in multi-trophic communities. Using species abundance data for 38 species over three years (from nine sites across central/eastern United States) and a novel tree-based inference method, we constructed seasonal networks for a multi-trophic freshwater stream fish community. We found that seasonality influences species interactions, particularly through rewiring (81%) as compared to species turnover (19%). Moreover, the number of rewiring interactions was best explained by fish status as a piscivore/non-piscivore and species maximum length ($R^2 = 0.41$). Our findings suggest that rewiring may be a dominant process in stream fish communities experiencing seasonal environments and that traits linked to trophic-level could be a good indicator of a species contribution to rewiring. As networks dominated by rewiring may be more robust, this network approach could be a valuable conservation tool for identifying which biological relationships must be retained for communities to avoid extinction.

Keywords: interaction networks, joint species distribution model, NEON data, seasonality

Introduction

Ecologists recognize that species interactions are a cornerstone in determining biodiversity and ecosystem functioning (Bascompte and Jordano 2007, Goudard and Loreau 2008). Particularly, species interactions are central in the evaluation of community stability which can be measured using a system's resilience, robustness and resistance to perturbations (Ives et al. 1999, Ives and Carpenter 2007, Donohue et al. 2013). Indeed, interactions can mediate the negative effects of environmental change (Brooker 2006, Suttle et al. 2007) and hence are essential for continued ecosystem persistence in the face of global change.

Species interactions vary across both space and time (Hagen et al. 2012, Rasmussen et al. 2013, Tylianakis and Morris 2017, Pellissier et al. 2018, Olivier et al.

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2019). Temporal heterogeneity, in particular seasonality, has been invoked to explain biodiversity and community structure (Tonkin et al. 2017). For example, seasonality has been shown to minimize competitive interactions and help stabilize total species abundances (Shimadzu et al. 2013), as well as play a role in maintaining structure and diversity in communities (Fitzgerald et al. 2017). Consequently, as environments experience regular seasonal oscillations (Tonkin et al. 2017), the influence of seasonality on species interactions is pervasive (McMeans et al. 2015).

From a community perspective, species interactions can be analyzed using network theory and seasonality can be incorporated by constructing and comparing separate species interaction networks representing different seasons (CaraDonna et al. 2017). The properties of seasonal species interaction networks can then be assessed based on their topological differences due to species turnover and interaction rewiring (i.e. the changes in the interactions between the same species across space or time despite both species remaining present) (Poisot et al. 2012). While seasonal species turnover or rewiring may be more dominant in a system, they act in concert (Alarcón et al. 2008, Petanidou et al. 2008, Olesen et al. 2011, CaraDonna et al. 2017, Schwarz et al. 2020). Identifying the relative contribution(s) of each to seasonal network topology is important as systems dominated by rewiring may be more robust to perturbations (Kaiser-Bunbury et al. 2010, Saavedra et al. 2016, Vizentin-Bugoni et al. 2020). Additionally, as traits have been shown to be an important driver of ecological network structure (Eklöf et al. 2013), determining how species traits relate to seasonal rewiring is a critical and unexplored component for understanding ecosystem dynamics.

Temperate freshwater stream ecosystems are well-suited to study the effects of seasonality as they experience regular seasonal variations from differences in shading, temperature, disturbance and productivity (Thompson and Townsend 1999). This strong influence of seasonality can have consequences for fish community assemblages (Junk et al. 1989, Peterson et al. 2017), making multi-trophic stream fish communities (Winemiller 1990, Peterson et al. 2017) an ideal system for studying seasonal rewiring. However, observational interaction data may not be accessible.

Indeed, due to the sampling effort required (Alarcón et al. 2008) and the difficulty in observing certain types of interactions (e.g. competition) (Faisal et al. 2010), few systems have the observational data required to produce observed temporal interaction networks. These challenges often restrain seasonal species interaction networks to few trackable system such as plant–pollinator networks (Alarcón et al. 2008, Petanidou et al. 2008, Olesen et al. 2011, Burkle et al. 2013, 2016, Rasmussen et al. 2013), but see Baird and Ulanowicz (1989), Yodzis and Winemiller (1999), Carnicer et al. (2009), Saavedra et al. (2016), Lopez et al. (2017), Peterson et al. (2017), McMeans et al. (2019) for notable exceptions.

To palliate the limitations related to direct interaction data, inferential methods that estimate species interaction networks have been proposed as an alternative to their empirically derived counterpart (Morales-Castilla et al. 2015). Inferential methods are reproducible, allow for a wider range of species given they require less sampling effort, and can detect interactions that are not readily observable (Faisal et al. 2010). While most inferred ecological interaction networks are constructed using species co-occurrence methods, they have been criticized for elucidating false interactions and for failing to detect true pairwise species interactions (Blanchet et al. 2020). A false interaction may arise due to species responding similarly to the same environmental factors (Peres-Neto et al. 2001) while true interactions may not be detected due to the coarseness of presence/absence data (Sander et al. 2017). Joint species distribution models (Pollock et al. 2014, Ovaskainen et al. 2016) have been touted as a more robust method to infer community structure as they incorporate abiotic factors into their analysis (D'Amen et al. 2018). However, these models are also often built using co-occurrence data and therefore suffer the same limitations as other methods that rely on presence/absence data to infer species interactions (Blanchet et al. 2020). A promising approach proposed by Momal et al. (2020) addresses limitations of presence/co-occurrence data by utilizing species abundances (instead of presence/absence data) and environmental covariates within a joint species distribution modeling framework. Including abundance measures provides richer information for capturing interactions (Blanchet et al. 2020) while the inclusion of environmental factors helps prevent spurious interactions in the network.

In this paper, we investigate seasonal changes in a multi-trophic freshwater stream fish community by creating seasonal networks using stream fish abundances (NEON 2020) and a novel tree-based inference method proposed by Momal et al. (2020). Using this method, we constructed two inferred fish interaction networks for Fall and Spring and examined their topological differences. Specifically, our objectives were to: 1) quantify the influence of seasonal interaction rewiring and species turnover (i.e. β-diversity); and, 2) evaluate whether seasonal changes in species interactions were related to species-specific traits.

Material and methods

Overview

Using the sampled freshwater fish abundances carried out by the National Science Foundation's National Ecological Observatory Network (NEON), we analysed abundance data by season (either Fall or Spring). Due to convergence issues in the network inference methods, yearly information had to be ignored during network construction. To ensure that year did not substantially influence the dynamics of the system, LASSO Poisson regressions (Friedman et al. 2010) were used to test the effect of year on species abundances. We found that the addition of year did not substantially improve the species abundance predications, allowing us to pool data based on the season the sample was taken. Inferred seasonal interaction networks were created via a two step-process: 1) construct Fall and Spring Poisson lognormal (PLN) models (Chiquet et al. 2018, 2019), a type of joint species distribution model that measure species interactions while controlling for environmental factors; and 2) apply the EMtree algorithm (Momal et al. 2020) which uses the fitted PLN models to create seasonal species interaction networks, using tree structured graphical models. We then quantified species turnover and rewiring using a measure of β-diversity (Poisot et al. 2012) across the two seasonal networks. Finally, we investigated (using linear regressions) how species-specific traits could be used to explain the total number of interactions classified as rewiring, and species turnover.

Fish data

Stream fish abundances were obtained from the 'Fish electrofishing, gill netting and fyke netting counts' dataset provided by NEON (2020). This dataset contains Fall and Spring stream fish abundances made via electrofishing under strict sampling protocols (Jensen et al. 2019). Additionally, this dataset included abiotic data such as environmental, geographic and sampling design factors (e.g. date of sampling, water temperature, dissolved oxygen, latitude) and fish length and fish weight data for each fish caught, for 28 aquatic monitoring locations across the United States.

To reduce yearly variation across seasons when pooling data into seasons, we only included sites that had consecutive seasonal measurements within a year, i.e. both Fall and Spring abundance measures made per year. Thus, our analysis used abundance samples from nine sites that spanned the United States, between 2017 and 2019 (Fig. 1).

The abundance dataset contained taxonomic information, but samples varied on the level of identification. Hence, we restricted our analyses to species with species-level identification as we were concerned that a higher taxonomic grouping would obscure key biological interactions. We excluded samples from the analysis if environmental conditions were not recorded.

For our trait analysis, we obtained species-specific traits from FishTraits (Frimpong and Angermeier 2009) and obtained species' maximum length and maximum weight from the NEON dataset containing the samples used to construct our networks. FishTraits is an extensive database that contained traits for our species except for *Etheostoma lachneri*, which we supplemented with those of *Etheostoma raneyi*, a

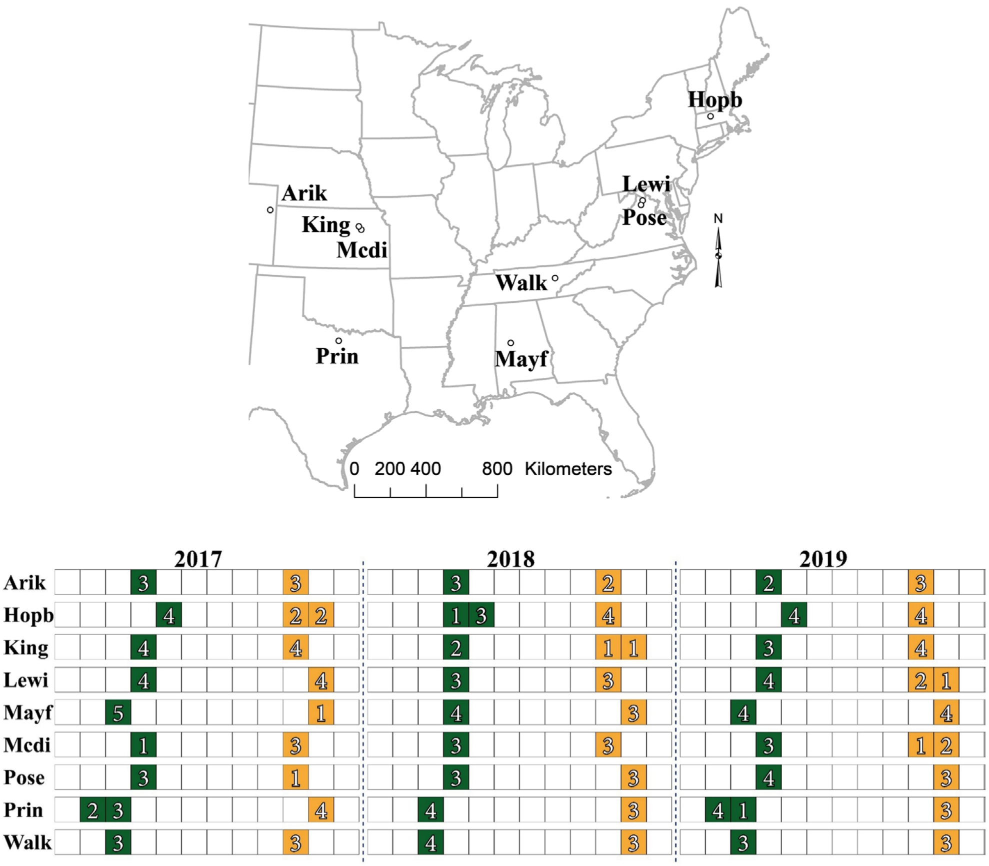

Figure 1. (Top) The nine NEON stream sampling locations across the United States used in this study; (bottom) monthly dates of freshwater fish abundance sampling for each of the nine sites used, where green boxes indicate Spring month dates, yellow boxes indicate Fall month dates, and the numbers inside the boxes are the number of days in which that month was sampled. Each day sampled represents multiple reaches sampled for abundances at that site.

Table 1. Fish feeding behaviours and total abundances for Fall and Spring in years 2017–2019.

		Total abundance				Total abundance	
Species	Feeding behaviours[†]	Fall	Spring	Species	Feeding behaviours[†]	Fall	Spring
Ameiurus melas	Herb, Invert	11	22	*Lepomis cyanellus*	Invert, Pisc	349	354
Ameiurus natalis	Herb, Invert, Pisc	64	53	*Lepomis macrochirus*	Invert	55	44
Campostoma anomalum	Herb	880	792	*Lepomis megalotis*	Invert, Pisc	32	52
Chrosomus erythrogaster	Herb	446	439	*Luxilus chrysocephalus*	Herb, Invert	31	
Clinostomus funduloides	Invert	65	200	*Micropterus salmoides*	Invert, Pisc		5
Cottus bairdii	Herb, Invert, Pisc	533	642	*Moxostoma carinatum*	Invert		15
Cottus carolinae	Invert, Pisc	134	193	*Nocomis leptocephalus*	Herb, Invert	86	35
Cottus girardi	Invert	796	953	*Notropis baileyi*	Invert	816	704
Etheostoma lachneri	Invert	73	301	*Notropis volucellus*	Herb, Invert		71
Etheostoma nigrum	Invert	301		*Noturus exilis*	Invert	98	98
Etheostoma spectabile	Invert	668	780	*Noturus funebris*	Invert	37	39
Etheostoma stigmaeum	Invert		38	*Noturus leptacanthus*	Invert	23	13
Etheostoma swaini	Invert		8	*Percina nigrofasciata*	Invert	69	37
Fundulus notatus	Herb, Invert	467	528	*Pimephales promelas*	Herb, Invert	150	163
Fundulus olivaceus	Herb, Invert	70	85	*Rhinichthys atratulus*	Invert	3559	3087
Gambusia affinis	Herb, Invert	1154	466	*Rhinichthys cataractae*	Invert		417
Hypentelium etowanum	Invert		13	*Salmo trutta*	Invert, Pisc	41	16
Ichthyomyzon gagei	Non-Feed	142	125	*Salvelinus fontinalis*	Invert, Pisc	84	53
Lampetra aepyptera	Non-Feed	131	170	*Semotilus atromaculatus*	Invert, Pisc	1328	938

[†] 1) Non-feed: non-feeding adults correspond to non-parasitic lamprey species, 2) Herb: herbivore, 3) Invert: invertivore and 4) Pisc: piscovore.

close relative (Ross 2012). Furthermore, we obtained feeding behaviour information from NatureServe (NatureServe 2020) where fish were classified as belonging to at least one of the following non-exclusive categories: 1) non-feeder (non-parasitic lamprey species), 2) herbivore, 3) invertivore and 4) piscivore (Table 1).

Testing for yearly abundance trends

We tested for yearly trends in each pooled seasonal dataset using LASSO Poisson regression models (Friedman et al. 2010) on each species data. LASSO Poisson models are a type of penalized generalized linear model for count data that forces less contributive coefficients to be zero. Generally, for each species we compared the predictive ability of 1) Site name and 2) Site name + Year, to test for yearly trends and to determine if pooling data across years into seasons was appropriate. Site name was included in both models to capture site-specific abiotic measurements as well as account for the variability of species presence/absence across sites. The withheld seasonal datasets used for predictive purposes included each site's most recent abundance sample for that season. We determined the 'best' model by calculating their predictive performance on the withheld dataset. We used two metrics for predictive performance: the cumulative root mean squared error (RMSE) and the cumulative RMSE for species with abundances greater than 0 in the prediction dataset ('RMSE obs > 0'). All LASSO Poisson regression models were implemented using 'glmnet' package (Friedman et al. 2010).

Constructing and testing Poisson lognormal (PLN) models

To model joint species abundances, required for inferring seasonal interaction networks, we first fitted and tested a suite of PLN models (Chiquet et al. 2018, 2019) on the pooled seasonal dataset. PLN models are joint species distribution models that can be used to infer joint species abundances and interactions using environmental factors and species' abundance data. Here, we built models that included different combinations of 1) water temperature during sampling, 2) dissolved oxygen during sampling, 3) specific conductivity during sampling, 4) elevation at sampling site, 5) date of abundance sampling, 6) latitude at abundance sampling and 7) site name. We also included sampling effort in our models as excluding this effort reduces the comparability of abundance samples measured at different places and times (Chiquet et al. 2019). Sampling effort was included for each abundance sample and was pre-calculated as a sum of the total counts of fish caught, a common approach for including sampling effort in models (Paulson et al. 2010). Altogether, the nine PLN models built for each season accounted for the following environmental variable(s): Site name, Water temperature, Dissolved oxygen, Elevation, Specific conductivity, Site name + Water temperature, Site name + Dissolved oxygen, Site name + Elevation and Site name + Specific conductivity.

We evaluated our seasonal PLN models by using non-traditional Bayesian information criterion (BIC), an information–theoretic approach; and by calculating their predictive performance on withheld future abundance data. Note the non-traditional BIC scores represent the variational lower bound of the BIC, which account for the model's variational log-likelihood and its number of parameters (see Momal et al. 2020 for more details). Overall, higher scores indicate better fitting models. To assess predictive performance, we predicted species abundances and compared the RMSE and RMSE obs > 0. The models with the best BIC score and lowest RMSE scores were the models selected. As we use both an in-sample and out-of-sample measurement (i.e. information–theoretic techniques and RMSE on withheld data), the models should have higher accuracy and lower uncertainty (Bodner et al. 2020). All construction and testing of PLN models were done through the 'PLNmodels' package (Chiquet et al. 2018, 2019).

Species interaction networks from EMtree

Separate Fall and Spring species interaction networks were inferred using the EMtree method proposed by Momal et al. (2020). Generally, EMtree combines both 1) PLN models to represent the joint distribution of species abundances and 2) spanning tree graphical models to create undirected species interaction networks, where a spanning tree is defined as a subgraph of a network that connects all nodes with the minimum number of possible connections (Dale and Fortin 2014). Note that while the number of interactions between all nodes is minimized and the minimum bound on the number of interactions a node may have in a tree is one, a node may have more than one or two interactions.

Network inference can be challenging due to the huge number of possible graphs for a given set of nodes (e.g. 10^{13} undirected graphs given 10 nodes). All network inference approaches try to infer the underlying true network configuration but are impeded by this vast number of configurations (Momal et al. 2020). To overcome this issue, EMtree employs a spanning tree-based approach, which is a technique designed to reduce the possible number of configurations given by the PLN model's joint distribution of abundances, to make inference tractable in the graph space (Momal et al. 2020). The links in the spanning tree represent possible interactions between species. EMtree constructs fitted species interaction networks by averaging across all spanning trees and employs an advanced tree-based algorithm to maximize the likelihood of the inferred species interactions from the PLN models. The EMtree approach combines both pairwise potential direct (e.g. predator–prey interactions) and indirect (e.g. indirect competition) interactions, represented as a single undirected connection between species' nodes. In the resulting networks, each connection was weighted with a value between zero and one, representing the conditional probability of each connection being part of the 'true' underlying network. We assumed that if an interaction had a non-zero weight, i.e. it is suspected to be part of the network, it existed in the network.

To create the network, it was necessary to select a minimum threshold as a cut-off for inferring species connections. This threshold can be used as a metric for assessing the reliability of connections with higher thresholds indicating higher reliability. Nonetheless, a guideline is to use the highest threshold before a node (i.e. species) loses all connections (Bassett et al. 2006). From a biological perspective, a connected network can emerge when just a few generalist species are present (Martín González et al. 2010). Hence, we created networks using thresholds between 0; the minimum possible threshold assuming virtually all connections, and 1; the maximum possible threshold producing no connections, and chose the network built with the highest threshold that remained connected. We increased network robustness by iteratively resampling the network 100 times. The EMtree approach was implemented using the 'EMtree' package (Momal et al. 2020), and network visualization was accomplished through the 'igraph' package (Csárdi and Nepusz 2006).

Beta diversity

To estimate species turnover and rewiring in our seasonal networks, we quantified the β-diversity across Fall and Spring. We adopted a β-diversity metric, β_{WN}, which measured the interaction turnover between two networks, with $0 \le \beta_{WN} \le 1$ (Poisot et al. 2012). This metric can be represented by the following equation:

$$\beta_{WN} = \frac{a+b+c}{\left(2a+b+c\right)/2} - 1 \tag{1}$$

where a was the number of interactions shared between networks (Fall and Spring), and b and c were the number of interactions unique to each network, respectively. Hence, larger values of β_{WN} indicated a greater difference between the two networks. We further isolated the effects of species turnover, β_{ST} and rewiring, β_{RW}, from β_{WN} using the equation $\beta_{WN} = \beta_{ST} + \beta_{RW}$. Additionally, we assessed total species dissimilarity between seasons (β_S) using Eq. 1, where a, b and c were the appropriate species identities.

Total species turnover, total rewiring and species traits

To calculate the total number of species turnover and rewiring connections for each species, we identified each changing connection in each seasonal network as being one of the following: 1) 'rewiring', where two species present in both seasons were linked in one season but not in the other; or 2) 'species turnover', where one or both species were present only in a single season, and the connection existed only for a single season. All connections preserved across seasons were classified as 'maintained'.

Using linear models, we examined the relationships between the total number of rewiring (i.e. sum of the connections classified as rewiring), and the total number of species turnover connections (i.e. sum of the connections classified as species turnover), with species traits, abundances, feeding preferences/trophic-level and habitat preferences.

All analyses conducted were done in R ver. 4.0.2 (R Core Team).

Table 2. Model fit (BIC scores, pseudo-R^2), and prediction error (RMSE, RMSE obs > 0) for each Poisson lognormal (PLNmodels) and Poisson regression model (glmnet) using $n = 32$ species for Fall data, and $n = 34$ for Spring data. Models were constructed using 74 (Fall) and 94 (Spring) observations where a single observation is a single sampling abundance measure for multiple species made at a specific point in a stream at one of the nine NEON sampling locations at a specific day. 'RMSE' (root mean square error) indicates the predictive ability of each model and predicts for $n = 32$ (Fall) and $n = 34$ (Spring) species based on the most recent observations for each of the nine NEON sites ($n = 288$ [Fall] and $n = 306$ [Spring]). 'RMSE obs > 0' indicates the predictive ability (root mean squared error) of each model for presence-only abundances (i.e. observations > 0) ($n = 38$ [Fall] and $n = 36$ [Spring]).

	Model type	Variables	BIC score	RMSE	RMSE obs > 0	R^2
Fall	PLN	Site name	−6418.470	4.230	11.107	0.93
		Site name + Water temperature	−6472.502	6.093	16.285	0.93
		Site name + Dissolved oxygen	−6456.427	6.138	16.548	0.92
	glmnet	Site name		10.353	27.135	
		Site name + Year		17.935	34.019	
Spring	PLN	Site name	−8158.602	5.004	12.365	0.94
		Site name + Water temperature	−8236.974	6.663	18.038	0.94
		Site name + Dissolved oxygen	−8219.048	4.900	12.897	0.94
	glmnet	Site name		7.350	19.722	
		Site name + Year		7.112	19.276	

Results

Data

We restricted our analysis to species that appeared in a seasonal dataset at least five times as fewer than five occurrences resulted in convergence issues when using the EMtree algorithm. This restriction resulted in 32 species in the Fall, 34 species in the Spring, with 29 species common to both seasons (Table 1), which contributed to a seasonal species dissimilarity score of $\beta_S \approx 0.134$.

Testing for yearly abundance

In the Fall, the LASSO Poisson regression of Site name [RMSE: 10.353, RMSE obs > 0: 27.135] performed better than Site name + Year [RMSE: 17.935, RMSE obs > 0: 34.019] (Table 2). Furthermore, in the Spring, the LASSO Poisson regression model of Site name [RMSE: 7.350, RMSE obs > 0: 19.722] performed equally well as Site name + Year [RMSE: 7.112, RMSE obs > 0: 19.276] (Table 2). Hence, Year did not contribute significantly to predicting Fall or Spring abundances and thus yearly variation was not deemed as a significant factor for either season.

PLN models

Using each respective pooled seasonal datasets, the three PLN models with highest BIC scores for both seasons were Site name (Fall BIC: −6419, Spring BIC −8159), Site name + Water temperature (Fall BIC: −6473, Spring BIC: −8237) and Site name + Dissolved oxygen (Fall BIC: −6456, Spring BIC: −8219) (Table 2). Site name also had the best BIC score and predictive performance in both the Fall (RMSE: 4.2, RMSE obs > 0: 11.1) and Spring (RMSE: 5.0, RMSE obs > 0: 12.4). Hence, the Site name PLN models, representing the inherent abiotic and spatial factors not measured at each site, were selected as best for both seasons.

Inferred seasonal networks from EMtree

We inferred each seasonal species interaction networks using EMtree paired with the Fall and Spring Site name PLN models (Fig. 2). We tested potential threshold cut-offs for each network and determined the highest appropriate threshold to be 0.6, since above this value the network became disconnected. Furthermore, as many species in our community are generalists, we expected that the underlying network to be connected (Martín González et al. 2010). Thus, all network metrics presented correspond to seasonal networks constructed with a threshold of 0.6.

Beta-diversity

The topological changes across seasons were apparent when quantifying topological change using β-diversity metrics. Specifically, interaction turnover was $\beta_{WN} \approx 0.62$. In other words, there was a relatively large difference in the topology of the Fall and Spring networks. This seasonal topological change was largely driven by interaction rewiring (β_{RW}) rather than species turnover (β_{ST}). In particular, we found that $\beta_{RW}/\beta_{WN} \approx 81\%$, whereas $\beta_{ST}/\beta_{WN} \approx 19\%$.

Total species turnover, total rewiring and species traits

Using linear regression models, we investigated how different species traits and abundances influenced the total number of rewiring (blue bars of Fig. 3). While we did not find any meaningful models regarding key life history traits or species' abundances, we found that species traits related to maximum length and feeding helped explain around 41% of the total number of rewiring. Specifically, total number of rewiring had a significant and negative relationship with a species' piscivore status and a significant positive relationship with the interaction between maximum length of a species and its piscivore status, Fig. 4 ($\beta_{\text{max length}} = -0.03$, $p > 0.1$; $\beta_{\text{piscivore}} = -6.10$, $p < 0.01$; $\beta_{\text{max length} \times \text{piscivore}} = 0.04$, $p < 0.01$;

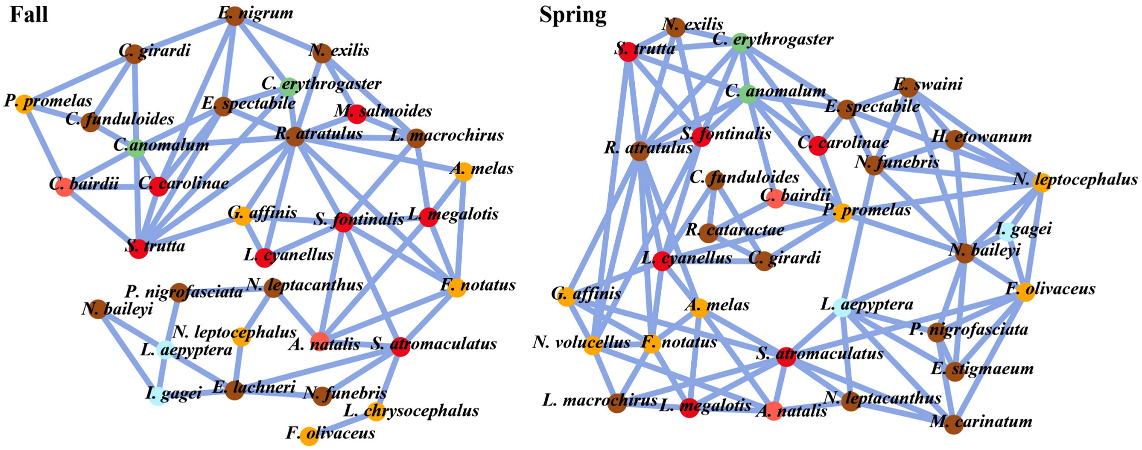

Figure 2. Threshold 0.6 of the Fall interaction network (n = 32 species) and the Spring interaction network (n = 34 species) of a freshwater fish stream community across nine sampling locations in the United States. Node colour corresponds to species feeding behavior: 1) light blue: non-feeding adults, 2) red: invertivore and piscivore, 3) light green: herbivore, 4) brown: invertivore, 5) dark yellow: herbivore and invertivore and 6) salmon: herbivore, invertivore and piscivore.

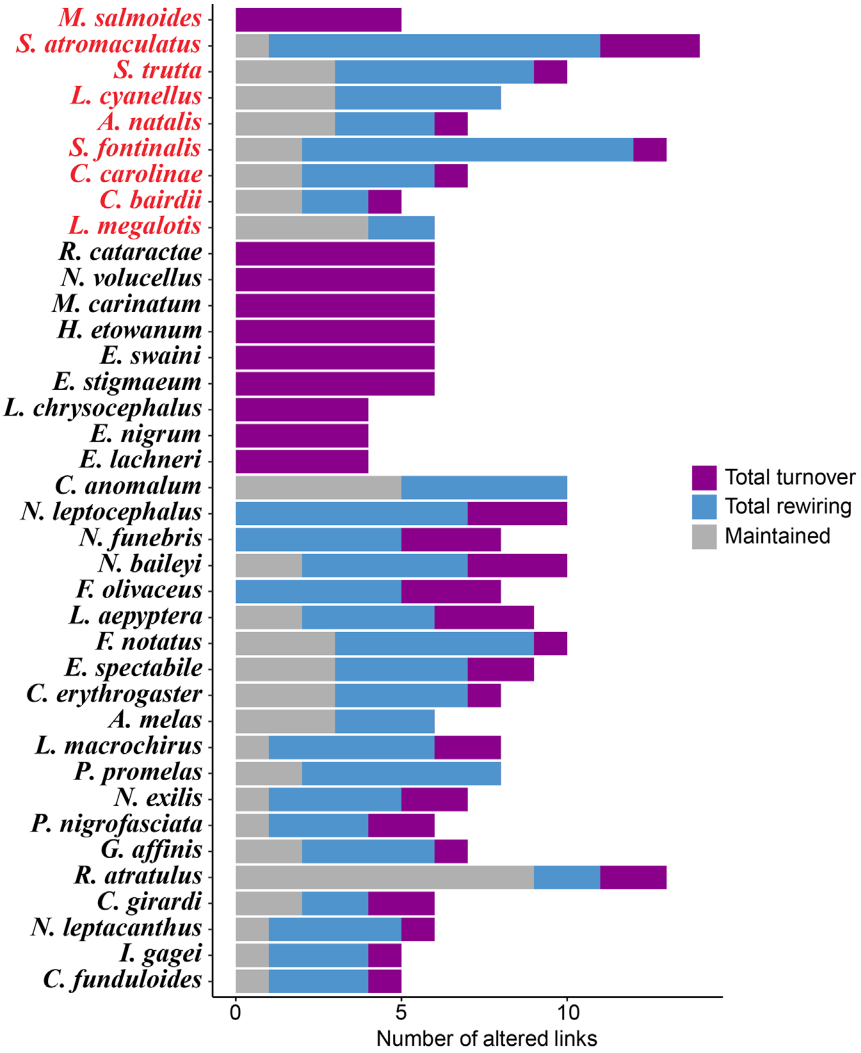

Figure 3. Number of maintained interactions and altered interactions for piscivores (red text) and non-piscivores (black text), including total number of rewiring (blue) and total number of species turnover interactions (purple), in each season using a network threshold of 0.6.

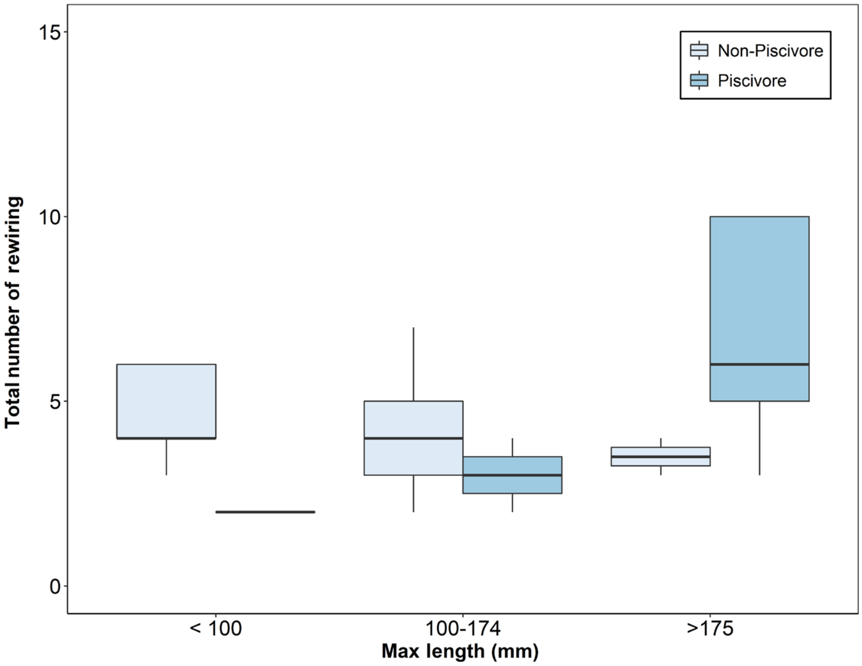

Figure 4. Relationship between the maximum length of the fish species (in mm) and its status as a piscivore against the total number of inferred rewiring for each species, using a network threshold of 0.6. For non-piscivores, the maximum length of the species appears to have a negligible effect on the total number of rewiring, however for piscivores, there appears to be a strong positive relationship indicating that the greater the maximum length of the species, the greater the total number of rewiring for that species (non-piscivore: n = 20, with n = 5, n = 13 and n = 2 for max length levels, respectively, and piscivore: n = 8, with n = 1, n = 2 and n = 5 for max length levels, respectively).

adjusted $R^2 = 0.41$). The negative relationship between piscivore status and the total number of rewiring suggested that non-piscivores have a greater number of rewiring than piscivores when controlling for the maximum length of a species. Interestingly, despite maximum length not being significant, its interaction with piscivore status is significant indicating that for piscivores, there is a strong positive relationship between the total size and the number of rewiring that does not exist for the non-piscivores.

We also note that while no specific traits or species abundances explained the total number of species turnover connections (purple bars of Fig. 3), approximately 80% of fish present for only a single season had preferences for large rivers. This percent is significantly higher than the approximately 45% of the non-turnover fish that shared this preference.

Discussion

The role of seasonality in shaping species interaction networks requires better assessment for understanding the stability and function of community assemblages. So far, most studies analyzed seasonality in small-size organismal bipartite networks (e.g. plant–pollinator networks), yet limited evidence exists on how seasonality shapes multi-trophic networks across communities of larger species. Despite increasing evidence that topological changes arise due to rewiring and species turnover (Alarcón et al. 2008, Petanidou et al. 2008, Rasmussen et al. 2013, Lopez et al. 2017, Schwarz et al. 2020), as of yet, identifying which process is dominant and more critically, quantifying the contributions of each process, is rarely done across seasons for multi-trophic networks. Here, we provide a study on inferred seasonal multi-trophic networks that provides evidence of seasonal change using interaction turnover, and that seasonal rewiring may be a driving process of community changes in stream fish communities.

Given the strong evidence of seasonality in stream fish networks (Thompson and Townsend 1999, Peterson et al. 2017), unsurprisingly, we found evidence that seasonality influenced our network structure. Indeed, the reported seasonal consumption of the most abundant aquatic invertebrates (Pinto and Uieda 2007), and the seasonal dietary shifts of ominvirous and carnivorous fish (Akin and Winemiller 2006) highlight the seasonal opportunistic feeding behaviour of many fish species. The differences in network structure we found between seasons are exemplified by the degree of its interaction turnover across seasons. As a score of zero indicates networks are identical and a score of one indicates that networks have no common interactions, our score of $\beta_{WN} = 0.62$, indicates a relatively high differentiation between our seasonal networks.

Beyond classifying network change, identifying the primary drivers of species interactions is essential for predicting community structure. In our study, we found that seasonal topological changes to our inferred network were primarily driven by interaction rewiring (81%) with a small contribution by species turnover (19%). Consequently, the level of rewiring and turnover we found in our study mirrors results from other systems. In particular, the amount of seasonal rewiring and seasonal turnover in our study is comparable to the weekly and mean yearly interactions found in the rewiring-dominated plant–pollinator networks studied by CaraDonna et al. (2017). While the ratio of seasonal species to those present in both seasons in our study is lower, this difference in species dissimilarity is likely in part the result of our requirement that species need to be sampled at least five times. The inclusion of these rare species would likely increase our species dissimilarity measure but would not have changed our overall network structure since they need to be abundant enough to warrant interactions (Poisot et al. 2015). Thus, our study contributes to the growing literature of the potential ubiquity of rewiring across different systems. However, we recognize that high levels of rewiring may be more common in some systems. Therefore, we hope future studies continue to quantify rewiring across study systems to further test its ubiquity and to identify cases and species where it may not be as dominant.

Despite highlighting the need to resolve networks along a temporal dimension, our results provide a general prediction for how these seasonal communities may respond to disturbances. If species subject to seasonality are more strongly driven by rewiring, we may also expect these species to be more robust when subject to other types of disturbances (CaraDonna et al. 2017). For example, Kaiser-Bunbury et al. (2010) found that in plant–pollinator networks, rewiring increased community robustness when faced with community species loss, Saavedra et al. (2016) found that seasonal interactions play a key role in maintaining the homeostatic state of ecological communities, and Vizentin-Bugoni et al. (2020) found that rewiring increased estimated robustness in plant–humming bird networks. Indeed, it would be of interest to conservation managers to determine if their systems are robust to future perturbations, given that their system also undergoes seasonal rewiring. However, while in general we expect rewiring to have a stabilizing effect, rewiring has been shown in some cases to have a negative effect on the persistence of both natural and computer-generated food webs (Gilljam et al. 2015). Hence, future studies should explore whether stability due to rewiring holds for different disturbance types, different ecosystems/organisms, and under which conditions it switches from a stabilizing to a destabilizing effect.

Total rewiring, total turnover and species traits

As fish species' traits may have high plasticity (Frimpong and Angermeier 2010), detecting relationships between traits and fish interaction dynamics can be an especially arduous task. Furthermore, given that rewiring can be both an active and/or passive process, it is perhaps especially difficult to identify key traits describing their ability to rewire. For example, a predator will actively rewire when it switches a prey item, whereas its prey passively rewires in response. In this case, we do not expect the predator and prey to exhibit the same traits. As traits related to the passive and active process of rewiring likely differ, we do not expect to find an all-encompassing relationship between any single trait and the total number of rewiring.

Nevertheless, the significant relationship we found between the total number of rewiring and the interaction between the maximum length of a species and its piscivore status ($R^2 = 0.41$) likely captures traits associated with active rewiring. Indeed, larger species of piscivores generally do consume a larger range of prey size than their smaller counterparts (Gaeta et al. 2018). This active rewiring may also capture the stabilizing ability of piscivores. Since these large mobile predators are able to track and exploit multiple abundant prey across multiple trophic levels, piscivorous fish can promote food web stability through reduced interaction strength and reduced predation pressure when prey density is low (Kondoh 2003, McCann et al. 2005). In addition, when maximum length was held constant, we also captured a significant negative relationship between piscivore status and the total number of rewiring. This negative relationship indicates that overall, non-piscivores have a higher total number of rewiring which may be in part due to many smaller non-piscivores passively rewiring with a few larger key predators. Additionally, as our network captures more than food web dynamics, this negative relationship may also be capturing rewiring due to competition and other biological interactions. If this is the case, lower trophic levels may be more heavily competing with different species for space and food across seasons whereas piscivores may maintain competitive interactions with the same species year-round.

We were unable to find any significant traits related to species turnover. This is not particularly surprising as unlike rewiring interactions, turnover interactions are dependent upon the arrival and departure of only nine species in our system. We expect that an increased species turnover rate would allow for relevant traits to be more easily detected. Despite not finding any significant traits related to the total turnover interactions, interestingly, all turnover species were those that preferred large rivers. Given this, we suspect that these turnover fish species may be seasonally migratory.

Limitations

The main limitation of our study is the dependence on inferred interactions from abundance data. As there are no direct observations of the interactions, there is always the possibility that these interactions do not exist. However, the benefits of approaches like the one used here, should not be overlooked. Despite there being no direct observations in our system, the inferred network approach allowed us to hypothesize seasonal networks for a previously unexplored community. In general, inferred network approaches not only allow us to reduce the resources required to infer species interactions but can propose interactions when observation is difficult (Faisal et al. 2010). Indeed, in our inferred seasonal network, we detected an interaction between *S. trutta* and *S. fontinalis* which had been hypothesized and only captured through experimental manipulation (Fausch and White 1981). Given that *S. trutta* and *S. fontinalis* are heavily monitored, we could validate our proposed interaction. However, most fish species are allocated fewer resources so there is little information available, particularly on their interactions. Ultimately, the inferred network approach allows us to generate new hypotheses about how these unobserved species may be interacting. The next steps forward could be to validate some of these key inferred interactions using experiments or in the case of predator–prey interactions, gut content analysis.

Another potential limitation in our study is the pooling together of yearly data (Jordán and Osváth 2009). Ideally, we would have constructed networks for each season per year without pooling data, allowing us to accommodate both yearly and seasonal variation in our networks. However, given the data available, this was not possible given convergence issues. To address the potential for yearly variation, we limited sites to those that had every seasonal abundance measurement between 2017 and 2019 and also ensured there were no substantial yearly trends in the abundance data using LASSO Poisson regression. In future, data collection efforts for these types of analyses should seek to collect greater abundance data per year such that both seasonal and yearly networks can easily be created.

Applications

Given the increasing availability of temporal abundance measurements, the robust EMtree approach we use here will likely be a valuable tool in the future to further disentangle species interaction networks. In particular, since it has been suggested that food webs rewire in predictable ways due to climate change (Bartley et al. 2019), this method may be used to investigate how interaction networks rewire in response to climate change where species interaction information is not available. Moreover, since it is widely recognized that interactions are the architecture of biodiversity (Bascompte and Jordano 2007), the maintenance of these interactions, even those that are seasonal, is a necessity to maintain ecosystem stability. In this regard, the approach we adopted for our analysis could be valuable for conservation as it can be used to hypothesize key biological relationships that must be retained for species to avoid extinction (Heinen et al. 2020).

Conclusion

The approach we take for network inference highlights the utility of non-traditional methods (e.g. species abundance data) to infer interactions and thus community structure. Although our network inference is not without its uncertainties, we demonstrate how EMtree methods can be used to elucidate network structure. Overall, we find evidence that differences in our seasonal networks appear to be driven mainly by rewiring as compared to species turnover. Additionally, while there is recognition that traits are important factors of community assembly our findings that maximum length and piscivore status contributes to a species' number of rewiring provide evidence that traits may influence how temporal interaction networks change. Finally, our study highlights the need to consider communities as evolving through time. Since seasonal change is capable of dramatically altering network topology, failing to capture temporal heterogeneities may cause us to mischaracterize community structure and functions.

Data availability statement

This study did not generate new data. The sources of the data used in this study were cited in the paper.

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Author contributions

Christopher Brimacombe: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Validation (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Korryn Bodner**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Marie-Josée Fortin**: Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

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