

Seasonal interactions and rewiring in freshwater stream fish networks

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Abstract

Despite evidence that seasonal variation may lead to the persistence of competing species, studies on the effect of seasonality on community network structures are limited. Furthermore, identifying whether seasonal network changes are the result of species turnover or rewiring (rearrangement of interactions among species), also remains understudied. Here, we investigate seasonal network changes in a stream fish community across Fall and Spring data. We find strong evidence that seasonality influences species interactions, particularly through rewiring. Moreover, we find that a species' number of rewiring interactions was best explained by its status as a piscivore/non-piscivore and its maximum length. Overall, we argue that rewiring may be a dominant process in communities experiencing seasonal environments and that traits linked to trophic-level may identify species contributing most to rewiring. As networks dominated by rewiring may be more robust, understanding the causes of changes in species interactions can help determine when communities may persist given a disturbance.

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Abstract: Despite evidence that seasonal variation may lead to the persistence of competing species, studies on the effect of seasonality on community network structures are limited. Furthermore, identifying whether seasonal network changes are the result of species turnover or rewiring (rearrangement of interactions among species), also remains understudied. Here, we investigate seasonal network changes in a stream fish community across Fall and Spring data. We find strong evidence that seasonality influences species interactions, particularly through rewiring. Moreover, we find that a species' number of rewiring interactions was best explained by its status as a piscivore/non-piscivore and its maximum length. Overall, we argue that rewiring may be a dominant process in communities experiencing seasonal environments and that traits linked to trophic-level may identify species contributing most to rewiring. As networks dominated by rewiring may be more robust, understanding the causes of changes in species interactions can help determine when communities may persist given a disturbance.

Introduction

Ecologists recognize that species interactions are a cornerstone in determining biodiversity, community assembly, and ecosystem functioning (Bascompte & Jordano 2007; Goudard & Loreau 2008; Tonkin *et al.* 2017). Thus, species interactions have far reaching biological implications (Tylianakis *et al.* 2008). For instance, species interactions are used in the evaluation of community stability (Ives & Carpenter 2007) and hence are essential for determining community resilience and resistance to perturbations. In addition, positive species interactions have been shown to produce species-rich model communities among competitors supported by a single limiting resource (Gross 2008), and facilitate increased species richness in harsh environments (Cavieses & Badano 2009). As well, interactions have been shown to mediate the negative effects of environmental change (Brooker 2006; Suttle *et al.* 2007), and hence are likely essential for continued ecosystem persistence in the face of global change.

While species interactions vary across both space and time (Rasmussen *et al.* 2013), fewer studies have focused on the changes in temporal interactions (Alarcón *et al.* 2008; Thompson *et al.* 2012) despite evidence linking them to the coexistence of competing species (McMeans *et al.* 2020). More recently, 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 (e.g., Fitzgerald *et al.* 2017). Consequently, as many environments experience seasonal oscillations (Tonkin *et al.* 2017) with different community compositions being favoured across different seasons, the influence of seasonality on species interactions is widespread.

Typically, species interactions are analyzed using network theory (Rasmussen *et al.* 2013) and seasonality can be incorporated by constructing and comparing separate networks representing different seasons. Often these types of ecological interaction networks are constructed using species co-occurrence methods (Freilich *et al.* 2018). Traditionally, these approaches assume that species with significant co-occurrence have beneficial interactions while species with significant co-exclusion have negative interactions (Cazelles *et al.* 2016). However, co-occurrence data and their corresponding methods 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). More recently, joint species distribution models (e.g., Pollock *et al.* 2014; Ovaskainen *et al.* 2016) have been touted as a more robust method to infer community structure over other co-occurrence methods as they incorporate abiotic factors into their analysis (D'Amen *et al.* 2018). However, while this approach controls for environmental factors, it is still likely limited by its reliance on co-occurrence data to infer species interactions (Blanchet *et al.* 2020). A promising approach proposed by Momal *et al.* (2020) addresses these issues by utilizing species abundances, instead of presence/absence data, with a joint species distribution model. Including abundance measures provides richer information for capturing interactions (Blanchet *et al.*

2020) while the inclusion of environmental factors help prevent spurious interactions in the network.

One of the strong utilities of using species interaction networks are the many developed tools available for comparing networks (e.g., Delmas *et al.* 2019). Of particular interest are metrics that evaluate 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 one of these two processes may be more dominant in a system than the other, these processes are not mutually exclusive. For example, the temporal changes in plant-pollinator networks are the result of both species turnover and rewiring (Alarcón *et al.* 2008; Petanidou *et al.* 2008; Olesen *et al.* 2011) and not a singular process. Identifying the relative contribution(s) of each process to network topology is important as systems dominated by rewiring, rather than species turnover, may be more robust to perturbations (CaraDonna *et al.* 2017). Additionally, as traits have been shown to be an important driver of ecological network structure (Eklöf *et al.* 2013), determining how traits relate to rewiring is a critical component for understanding ecosystem dynamics.

Due to the sampling effort required, few systems have the appropriate biological data needed to produce temporal interaction networks (Alarcón *et al.* 2008). The difficulty of collecting large spatial or temporal-scale data primarily limits seasonal network analysis to physically small organisms such as those that make-up bipartite plant pollinator networks (e.g., Alarcón *et al.* 2008; Petanidou *et al.* 2008; Olesen *et al.* 2011; Rasmussen *et al.* 2013; Burkle *et al.* 2016; CaraDonna *et al.* 2017). However, notable exceptions include seasonal networks of tropical fish (Winemiller 1990), frugivorous birds (Carnicer *et al.* 2009), a forest predator-prey community (Saavedra *et al.* 2016), and a consumer-resource intertidal community (Lopez *et al.* 2017). Given the release of a recent time series dataset of stream fish abundances for sites across the United States (NEON 2020), there is a unique opportunity to investigate seasonal networks in a freshwater stream ecosystem. Since stream communities experience regular seasonal variations from differences in shading, temperature, disturbance, and productivity (Thompson & Townsend 1999), they are likely a valuable study system to understand the effects of seasonality on multiplex networks.

Here, we investigate seasonal changes in a freshwater stream fish community using NEON data (NEON 2020) and quantify both species turnover and interaction rewiring therein. Specifically, our objectives are to: (i) determine if there are measurable differences between Fall and Spring networks, using modularity and interaction turnover (i.e. beta-diversity); (ii) quantify the influence of interaction rewiring and species turnover in these communities; and, (iii) evaluate whether seasonal changes in species interactions are related to species-specific traits. To do so, we apply the recently proposed method of Moma *et al.* (2020) to construct two freshwater species multiplex networks for Fall and Spring. We find that: (i) Spring interaction networks have higher modularity than Fall networks, and between seasons, there is a large amount of interaction turnover; (ii) most topological change across seasons are the result of species rewiring (c.87%) as compared to species turnover (c.13%); and (iii) species' maximum length and its piscivore/non-piscivore status help explain a species total number of rewiring connections (adjusted $R^2=0.34$).

Materials and Methods

Using fish abundance data from NEON, we constructed seasonal interaction networks using a two step-process: (i) developed Fall and Spring Poisson log-normal (PLN) models to explain species abundances in each season, and (ii) adopted the EMtree approach that used the fitted PLN models to create nondirectional seasonal species interaction networks. We then quantified species turnover and rewiring using a measure of beta-diversity. Finally, we used linear regression models to explore how species-specific traits explained the total number of interactions classified as “rewiring”, and “species turnover”.

Fish Data

Fish abundance data were obtained from the “Fish electrofishing, gill netting, and fyke netting counts” dataset provided by the National Science Foundation’s National Ecological Observatory Network (NEON 2020). This dataset contains stream fish abundances as well as abiotic data including environmental, geographic, and sampling design factors (e.g., date of sampling, water temperature, dissolved oxygen, latitude) and biotic

data (e.g., fish length, fish weight) for 28 aquatic monitoring locations across the United States. Our analysis used samples from 2016–2019 collected twice per year per location, in Fall and Spring across subsequent days for 39 species—36 species in the Fall and 35 species in the Spring.

The abundance dataset contained taxonomic information, but samples varied on the level of identification. 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. Additionally, as sampling locations were established at different times, and not all locations had the same number of sampling observations, we removed sites that had less than seven sampling seasons to improve model convergence. Ultimately, we used nine sites that spanned the United States (Figure 1).

For our trait analysis, we obtained species-specific traits, such as longevity, and large river preference from Fishtraits (Frimpong & 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 close relative (Ross 2012). Furthermore, we obtained feeding behaviour information from NatureServe (NatureServe 2020) where fish were classified as belonging to one of the following non-exclusive categories: (i) non-feeder (non-parasitic lamprey species), (ii) herbivore, (iii) insectivore, and (iv) piscivore.

Constructing and Testing Poisson Lognormal (PLN) Models

To construct our seasonal interaction networks, we first fitted, and tested a suite of PLN models. PLN models are a type of joint species distribution model which uses abiotic factors and species’ abundance data to infer species joint abundances (Momal *et al.* 2020). To control for environmental effects, we built models that included different combinations of (i) water temperature during sampling, (ii) dissolved oxygen during sampling, (iii) date of abundance sampling, (iv) latitude, and (v) site name. We incorporated site name as a potential variable to account for any site-specific abiotic measurements not captured by other factors. 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 six PLN models built for each season accounted for the following environmental variable(s): *Site name*, *Water temperature*, *Dissolved oxygen*, *Site name + Latitude*, *Site name + Water Temperature*, and *Site name + Dissolved oxygen*.

To test our seasonal PLN models, we performed a two-step procedure: (1) evaluated models using non-traditional Bayesian Information Criterion (BIC), an information-theoretic approach; and, (2) validated the PLN models against withheld future abundance data. Although our objective was not to predict species abundances, by comparing models using information-theoretic techniques and by calculating their predictive performance on withheld future data, we could select models that had higher accuracy and lower uncertainty (Bodner *et al. in press*).

The BIC scores were calculated and PLN models with the worst scores per season were discarded. Note these are non-traditional BIC scores that represent the variational lower bound of the BIC, which account for the model’s variational log-likelihood and its number of parameters. Overall, higher scores indicate better fitting models. The top three seasonal PLN models with the highest BIC scores were then tested against the withheld dataset. We evaluated each of the top three model’s predictive capabilities by removing the two most recent sampling times for each site and season used as validation measures. We predicted species abundances and compared the predictions (using root mean squared error: “RMSE”) to the withheld validation datasets. We also calculated RMSE only for species with abundances greater than 0 (“RMSE obs>0”). From the three PLN models tested per season, each final seasonal model selected had the highest predictive ability as determined by RMSE and RMSE obs>0.

Species Interaction Network

To construct separate Fall and Spring nondirectional species interaction networks, we adopted the methods of EMtree as proposed by Momal *et al.* (2020). Generally, EMtree uses both (i) PLN models to represent the joint distribution of species abundances and (ii) spanning trees to create species interaction networks, where a spanning tree is defined as a subset of a network that connects all nodes with the minimum number of possible connections (Dale & Fortin 2014).

All network inference approaches try to reconstruct the underlying true network configuration, but are impeded by the vast number of configurations that a network may have (Momal *et al.* 2020). To overcome this issue, EMtree employs a tree-based approach to reduce the number of possible network configurations. EMtree constructs fitted species interaction networks by averaging across the 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. Each connection within the network 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, it existed in the network.

To create the network, we had 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. We evaluated our network using consecutive thresholds of 0.2 between 0.1 and 0.9 (0 is the minimum possible threshold assuming virtually all connections and 1 is the maximum possible threshold producing 0 connections). We increased network robustness by iteratively resampling the network 100 times. The EMtree approach was implemented using the EMtree package (Momal *et al.* 2020) in R version 3.6.0 (R Core Team 2020).

Network Metrics: Modularity

To better characterize seasonality in network structures, we used a betweenness community detection method (Newman & Girvan 2004) to create modules within each seasonal network. We evaluated the modularity of each seasonal network, using the equation:

$$Q = \frac{1}{2m} \sum_{i,j} \left(A_{ij} - \frac{k_i \bullet k_j}{2m} \right) \bullet \delta_{m_i, m_j},$$

where m are the total number of interactions in the network, A is the adjacency matrix of the network ($A_{i,j} = 1$ if there is an interaction between species i and j , otherwise 0), k_i are the number of interactions of node i , m_i is the module of species i , and δ is a Kronecker's delta ($\delta_{a,b} = 1$ if $a = b$, otherwise 0) (Stouffer & Bascompte 2011). Higher modularity values indicated that partitions between close knit groups were more easily detectable and meaningful within the community. Network visualization and modularity detection were both implemented using the *igraph* package R (Csárdi & Nepusz 2006).

Beta Diversity

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

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

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 $\beta_{\Omega N}$ indicated a greater difference between the two networks. We further isolated the effects of species turnover, β_{ST} , and rewiring, β_{PN} , from $\beta_{\Omega N}$ using the equation $\beta_{\Omega N} = \beta_{ST} + \beta_{PN}$.

Total Species Turnover, Total Rewiring, and 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: (i) “rewiring”, where two species present in both seasons were linked in one season but not in the other; or (ii) “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 rewirings (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.

Results

PLN Models

Given potential convergence issues with the PLN models, we restricted our analysis to species that appeared in the dataset at least four times in each season. This restriction resulted in 36 species in the Fall with four unique species (i.e. species found only in the Fall), and 35 species in the Spring with three unique species, and a total of 32 species present in both seasons (top panel of Figure 3).

The three PLN models with highest BIC scores in both Fall and Spring were *Site name*, *Site name + Water temperature*, and *Site name + Dissolved oxygen* (Table 1). For model validation in the Fall, the model with the lowest RMSE and RMSE obs>0 was *Site name + Water temperature*. Although *Site name* had the highest BIC score in the Fall, *Site name + Water temperature* had only a marginally lower score and it performed the best during model validation. Therefore, *Site name + Water temperature* was selected to construct the Fall species interaction network. In the Spring, *Site name* had both the highest BIC score as well as the best predictive performance, and was hence chosen as the best model for the Spring network.

Seasonal Network Reconstruction

Using the PLN models *Site name + Water temperature* and *Site name*, we constructed the species interaction networks for Fall and Spring, respectively. We tested potential threshold cut-offs for the networks as depicted in Momal *et al.* (2020). As there were no clear thresholds (see Figure S3), we applied a sequence of thresholds from 0.3–0.7 and generated separate seasonal networks. We limited the thresholds to 0.3 and above as thresholds below this value created very dense networks. Specifically, this threshold resulted in species connecting to, on average, around 40% of their network. As well, we limited the thresholds to 0.7 and below as thresholds above this value were too conservative, with many species having no connections. In the main text, we present seasonal networks constructed with a threshold of 0.5 (Figure 2) as this threshold balanced the trade-offs of over or under-estimating possible connections (see Supplementary Material for seasonal networks using the 0.3 and 0.7 thresholds). The subsequent results for β -diversity and our trait-based analysis were conducted for the three thresholds (0.3, 0.5, and 0.7) and their results can be found in the primary text.

Modularity

Seasonal topological changes to species interaction networks were apparent in the modularity values (Q_{Season}) across thresholds (Table 2). Particularly, at a threshold of 0.5, the modularity score in the Fall, $Q_{Fall} = 0.47$ (six modules; left panel of Figure 2), was lower than the Spring, $Q_{Spring} = 0.51$ (four modules; right panel of Figure 2), indicating that species in the Spring interacted with those classified as being part of their modules more so than species in the Fall. This difference between seasonal modularity was further exemplified in average modularity scores across all thresholds, with Fall, $Q_{Fall} = 0.45$, lower than the Spring, $Q_{Spring} = 0.52$.

Beta-diversity

The topological changes across seasons were also very apparent when quantifying topological change using β -diversity metrics (see Table 2). Specifically, at a threshold of 0.5, interaction turnover was $\beta_{P\Omega} = 0.56$, and increased with increased threshold values. In other words, there was a relatively large difference in the

topology of the Fall and Spring networks. Moreover, the average interaction turnover across all thresholds was even larger; $\beta_{WN} = 0.60$. These seasonal topological changes were largely driven by interaction rewiring ($\beta_{P\Omega}$) rather than species turnover (β_{ST}). In particular, at a threshold of 0.5, we found that $\beta_{RW}/\beta_{WN} \approx 84\%$ whereas $\beta_{ST}/\beta_{WN} \approx 16\%$. This indicates that 84% of interaction turnover was due to rewiring and 16% was due to species turnover. This effect of rewiring was even more dominant when averaging across all thresholds, $\beta_{RW}/\beta_{WN} \approx 87\%$, as compared to species turnover $\beta_{ST}/\beta_{WN} \approx 13\%$.

Total Species Turnover, Total Rewiring, and Traits

Using linear regression models, we explored how different species traits and abundances influenced the total number of rewirings (bottom panel of Figure 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 35% of the total number of rewirings. Specifically, total number of rewirings 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, Figure 4 ($\beta_{Max\ length * \text{piscivore}} = 0.39, p > 0.05$; $\beta_{\text{piscivore}} = -9.49, p < 0.01$; $\beta_{Max\ length * \text{piscivore}} = 0.05, p < 0.01$; adjusted $R^2 = 0.344$; Table S2). The negative relationship between piscivore status and the total number of rewirings suggested that non-piscivores have a greater number of rewirings than piscivores when controlling for the maximum length of a species. Interestingly, despite there being no overall effect of max length on the total number of rewirings, the significant interaction indicates that for piscivores, there is a strong positive relationship between the total size and the number of rewirings 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, all fish that contributed to species turnover ($n = 7$) had preferences for large rivers (compared to only 60% of the non-turnover fish). Furthermore, *Micropterus salmoides*, one of the seven turnover species, explained about 24% of the total number of species turnover connections at a threshold of 0.5 ($\beta_{\text{Micropterus salmoides}} = 7.136, p < 0.001; R^2 = 0.24$).

Discussion

The role of seasonality in shaping species interaction networks remains largely unexplored. While few studies have shown seasonality in small-size organismal bipartite networks (e.g., plant-pollinator networks), limited evidence exists on how seasonality shapes multiplex 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; Olesen *et al.* 2011; Rasmussen *et al.* 2013; Lopez *et al.* 2017), as of yet, identifying which process is dominant and more critically, quantifying the contributions of each process, is rarely done across seasons and for multiplex networks. Here, we provide a study on seasonal multiplex networks that shows strong evidence of seasonal change using both modularity scores and interaction turnover, and further show that seasonal rewiring is the main driving process of community changes in stream fish communities.

Given the long appreciated influence of temporal oscillations in theoretical ecology (e.g., Hutchinson 1961), as well as the strong evidence of seasonality in stream fish networks (e.g., Thompson & Townsend 1999), unsurprisingly, we found evidence that seasonality influenced our network structure. In particular, the arrangement of species into close knit groups (i.e. modules), was higher in the Spring than the Fall underscoring that species are assembling differently across seasons. Specifically, in the Spring, species on average confine their interactions more often to a subset of species (i.e. those in their module) as compared to species in the Fall. This may signify that communities in the Spring are more robust to perturbations as the effects of these perturbations may be confined to specific modules rather than spreading to the entire community (Gilaranz *et al.* 2017). The differences in network structure between seasons is also exemplified in 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 average score of $\beta_{WN} = 0.60$, indicates a relatively high differentiation between our seasonal networks. Taken together, both modularity and total interaction turnover metrics provides strong evidence that network topology is indeed changing across seasons.

Beyond classifying network change, identifying the primary drivers of species interactions is essential for predicting community structure (McLeod *et al.* 2020). In our study, we found that seasonal topological changes to our inferred network were primarily driven by interaction rewiring (c.87%) with a small contribution by species turnover (c.13%). Moreover, the contribution of species turnover to seasonal topological change ($\beta_{ST}/\beta_{\Omega N}$) was always smaller than the overall number of species that contributed to turnover; $7/32 \approx 0.22$. Generally, this low value for species turnover indicates that species only observed in a single season are not highly connected to other species. Our results contribute to the small but growing recognition that rewiring occurs at seasonal scales, and that a significant portion of interactions in an ecological network are transient (Carnicer *et al.* 2009; CaraDonna *et al.* 2017; Lopez *et al.* 2017).

Despite highlighting the need to resolve networks along a temporal gradient, our results regarding the potential dominance of rewiring across seasonal networks also provides 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, and Saavedra *et al.* (2016) found that seasonal interactions play a key role in maintaining the homeostatic state of ecological communities. 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, and under which conditions it switches from a stabilizing to a destabilizing effect.

Total Rewiring, Total Turnover, and Traits

As fish species' traits may have high plasticity (Frimpong & 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 a very strong relationship between any single trait and the total number of rewirings.

The significant relationship we found between the total number of rewirings and the interaction between the maximum length of a species and its piscivore status 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). In addition, when holding maximum length constant, we also captured a significant negative relationship between piscivore status and the total number of rewirings indicating that overall non-piscivores have a higher total number of rewirings. This negative relationship 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.

Interestingly, all species that contributed to species turnover and thus the total number of species turnover interactions, were those that also preferred large rivers. Given this, we strongly suspect that these fish may be seasonally migratory species. Regarding the total number of species turnover interactions, we were unable to find a specific trait that explains its variability. However, we found that *Micropterus salmoides* explained almost 25% of the total number of species turnover interactions. This result is not surprising as this species has been shown to exhibit trophic plasticity allowing them to be a successful invasive species even in stable food webs (Almeida *et al.* 2012).

Applications and Future Directions

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. Moreover, since it is widely recognized that interactions are the architecture of biodiversity (Bascompte & Jordano 2007), the maintenance of these interactions, even those that are seasonal, is a necessity to maintain current ecosystem stability. In this regard, the approach we adopted for our analysis could be valuable for conservation as it can be used to detect key biological relationships that must be retained for species to avoid extinction.

Future studies should seek to quantify the degree of temporal rewiring and species turnover, and the conditions under which these processes become the dominant topological change to communities. While species rewiring was dominant in our study, the processes which drive topological changes are context dependent, even for similar study systems. For example, changes in plant-pollinator networks have been attributed to both temporal species turnover and rewiring in some cases (Alarcón *et al.* 2008; Petanidou *et al.* 2008; Olesen *et al.* 2011), and in other cases, the majority of changes were attributed to rapid rewiring (CaraDonna *et al.* 2017). Nonetheless, given the potential implications of rewiring on stability, and robustness of network structure, we strongly advocate for its continued study to determine when and where temporal rewiring and species turnover are dominant.

Conclusion

The approach we take for network reconstruction highlights the utility of non-traditional methods (e.g., species co-occurrence data) to infer interactions and thus community structure. Moreover, through our indirect methods (i.e. abundance measurements over time), we captured potential interactions other than those that are amenable to direct observation. Although our network reconstruction is not without its uncertainties, we demonstrate how EMtree methods can be used to elucidate multiplex network structure. Overall, we find strong 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 (e.g., Kneitel & Chase 2004), our findings that maximum length and piscivore status contributes to a species' number of rewirings 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 true community structure.

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Figures:

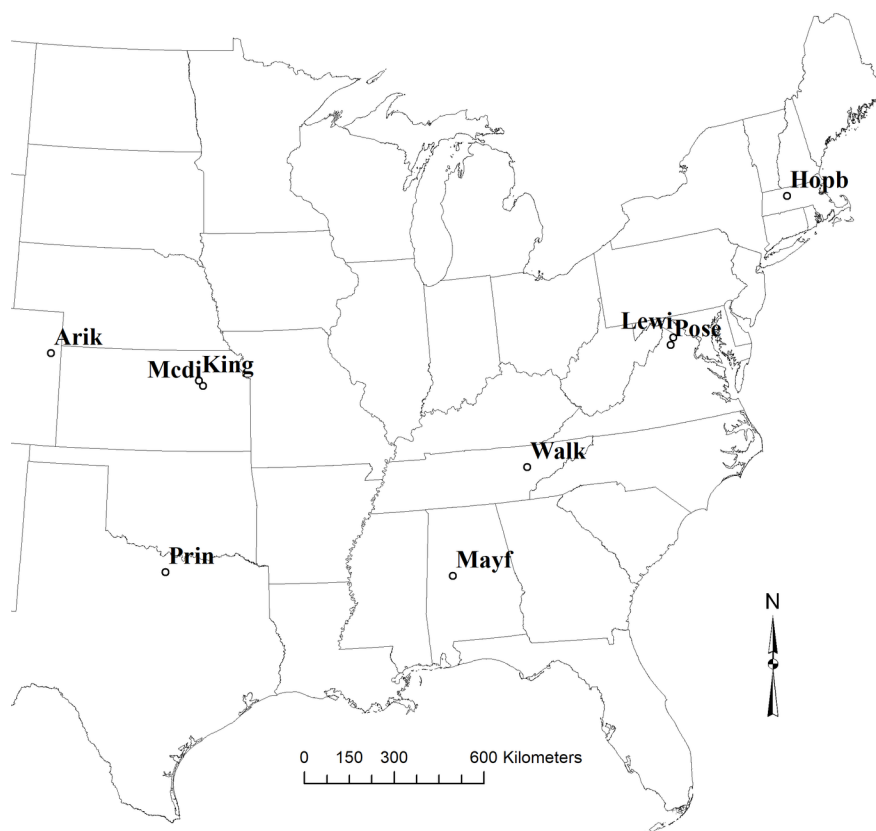
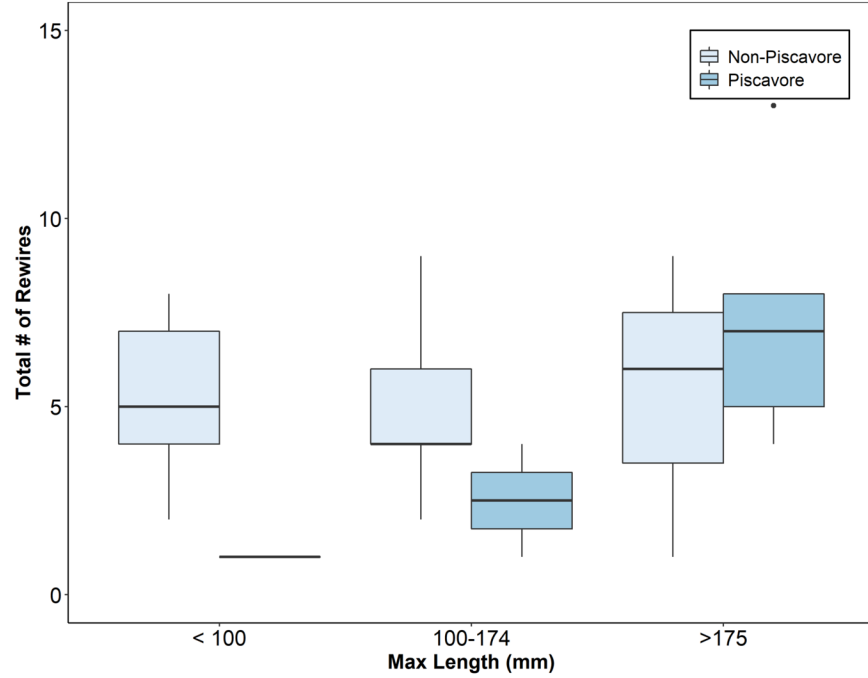


Figure 1. The nine NEON stream sampling locations used in this study.



Figure 2. Threshold 0.5 of (left) Fall interaction network (n=36 species) and (right) Spring interaction network (n=35 species) of a freshwater fish stream community across nine sampling locations in the United States. Different modules are delineated by grey modules. 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.



Tables:

Table 1. Model fit (BIC scores, adjusted R^2), and prediction error (RMSE, RMSE obs > 0) for each PLN model using $n = 36$ species for Fall data, and $n = 35$ for Spring data. Models were constructed using 78 (Fall) and 86 (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 36 (Fall) and 35 (Spring) species based on the two most recent observations for each of the nine NEON sites ($n = 648$ [Fall] and $n = 630$ [Spring]). “RMSE obs > 0” indicates the predictive ability (root mean squared error) of each model for presence-only abundances (i.e. observations > 0) ($n = 87$ [Fall] and $n = 79$ [Spring]).

	PLN model	BIC Score	RMSE	RMSE obs>0	R^2
Fall	<i>Site name</i>	-3723.85	20.18	54.05	0.93
	<i>Site name + Water temperature</i>	-3773.78	16.55	44.89	0.92
	<i>Site name + Dissolved oxygen</i>	-3767.27	23.92	64.52	0.92
	<i>Site name + Latitude</i>	-3794.34	22.50	60.80	0.92
Spring	<i>Site name</i>	-3679.88	7.08	17.16	0.94
	<i>Site name + Water temperature</i>	-3722.80	10.36	26.61	0.93
	<i>Site name + Dissolved oxygen</i>	-3737.11	10.99	29.40	0.93
	<i>Site name + Latitude</i>	-3751.83	6.81	16.01	0.94

Table 2. Beta-diversity (β) measures for different species interaction networks and modularity scores (Q_{Season}) across thresholds. $\beta_{\Omega N}$ is the interaction turnover between Fall and Spring networks; β_{PQ} is the amount of interaction change as a result of rewiring; and β_{ST} is the amount of changes as a result of species turnover.

Threshold	$\beta_{\Omega N}$	$\beta_{P\Omega}$	$\beta_{\Sigma T}$	Q_{Fall}	Q_{Spring}
0.3	0.54	0.44	0.10	0.37	0.46
0.5	0.56	0.47	0.09	0.47	0.51
0.7	0.70	0.64	0.06	0.52	0.59
Mean	0.60	0.52	0.08	0.45	0.52

Appendix:

Table S1. Fish feeding behaviours and total abundances for Fall and Spring in years 2016-2019.

Species	Feeding Behaviours+	Total Abundance	Total Abundance
		Fall	Spring
<i>A. melas</i>	Herb, Invert	7	22
<i>A. natalis</i>	Herb, Invert, Pisc	58	52
<i>C. anomalum</i>	Herb	740	774
<i>C. bairdii</i>	Herb, Invert, Pisc	398	642
<i>C. carolinae</i>	Invert, Pisc	124	193
<i>C. erythrogaster</i>	Herb	391	438
<i>C. funduloides</i>	Invert	57	185
<i>C. girardi</i>	Invert	647	903
<i>E. lachneri</i>	Invert	46	8
<i>E. nigrum</i>	Invert	301	
<i>E. spectabile</i>	Invert	568	730
<i>E. stigmaeum</i>	Invert	67	38
<i>E. swaini</i>	Invert	24	8
<i>F. notatus</i>	Herb, Invert	352	528
<i>F. olivaceus</i>	Herb, Invert	55	85
<i>G. affinis</i>	Herb, Invert	714	466
<i>H. etowanum</i>	Invert	5	13
<i>I. gagei</i>	Non-Feed	113	125
<i>L. aepyptera</i>	Non-Feed	102	170
<i>L. chrysocephalus</i>	Herb, Invert	26	
<i>L. cyanellus</i>	Invert, Pisc	219	352
<i>L. macrochirus</i>	Invert	46	43
<i>L. megalotis</i>	Invert, Pisc	25	52
<i>M. salmoides</i>	Invert, Pisc	4	
<i>M. carinatum</i>	Invert		15
<i>N. baileyi</i>	Invert	654	704
<i>N. crysoleucas</i>	Herb, Invert	6	
<i>N. exilis</i>	Invert	90	81
<i>N. funebris</i>	Invert	21	39
<i>N. leptacanthus</i>	Invert	18	12
<i>N. leptcephalus</i>	Herb, Invert	75	35
<i>P. nigrofasciata</i>	Invert	60	37
<i>N. volucellus</i>	Herb, Invert		71
<i>P. promelas</i>	Herb, Invert	117	163
<i>R. atratulus</i>	Invert	2753	2857
<i>R. cataractae</i>	Invert		608
<i>S. atromaculatus</i>	Invert, Pisc	1236	917
<i>S. fontinalis</i>	Invert, Pisc	188	53

		Total Abundance	Total Abundance
<i>S. trutta</i>	Invert, Pisc	70	16

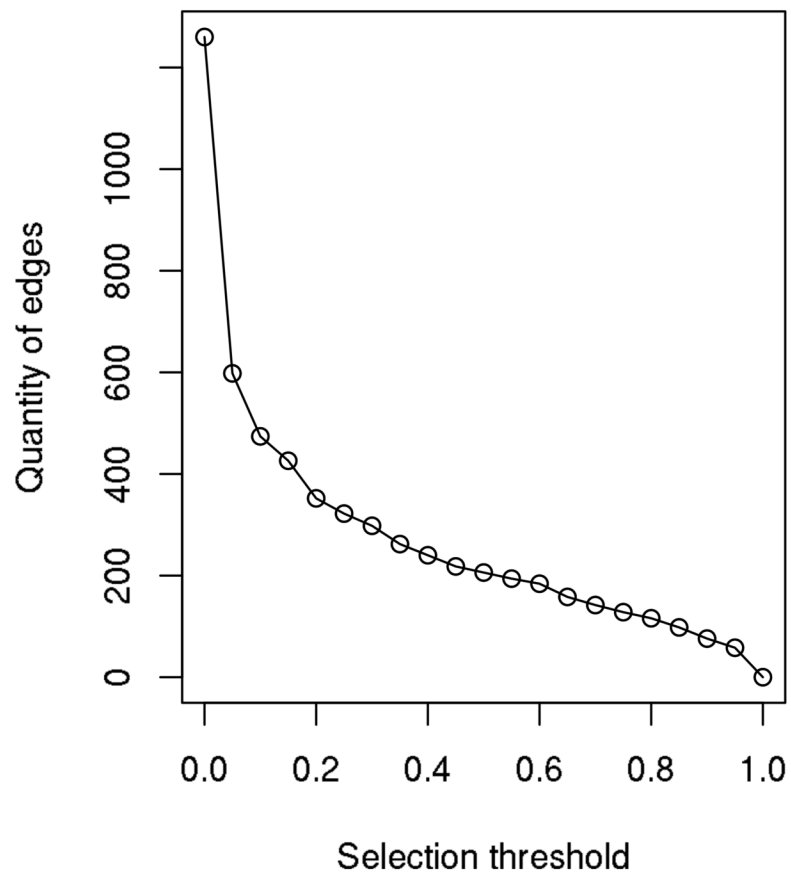
+ (1) *Non-Fed*: non-feeding adults correspond to non-parasitic lamprey species, (2) *Herb*: herbivore, (3) *Invert*: insectivore, and (4) *Pisc*: piscovore.



Figure S1. Threshold 0.3 of [left] Fall interaction network with n=36 and [right] Fall interaction network with n=35 freshwater stream fish species across nine sampling locations in the United States, where modules are delineated in grey. Node colour corresponds to species feeding behavior: (1) light blue: non-feeding adults, (2) red: invertivore, and piscovore, (3) light green: herbivore, (4) brown: invertivore, (5) dark yellow: herbivore, and invertivore, and (6) salmon: herbivore, invertivore, and piscovore.



Figure S2. Threshold 0.7 of [left] Fall interaction network with n=36 and [right] Spring interaction network with n=35 freshwater stream fish species across nine sampling locations in the United States, where modules are delineated in grey. Node colour corresponds to species feeding behavior: (1) light blue: non-feeding adults, (2) red: invertivore, and piscovore, (3) light green: herbivore, (4) brown: invertivore, (5) dark yellow: herbivore, and invertivore, and (6) salmon: herbivore, invertivore, and piscovore.



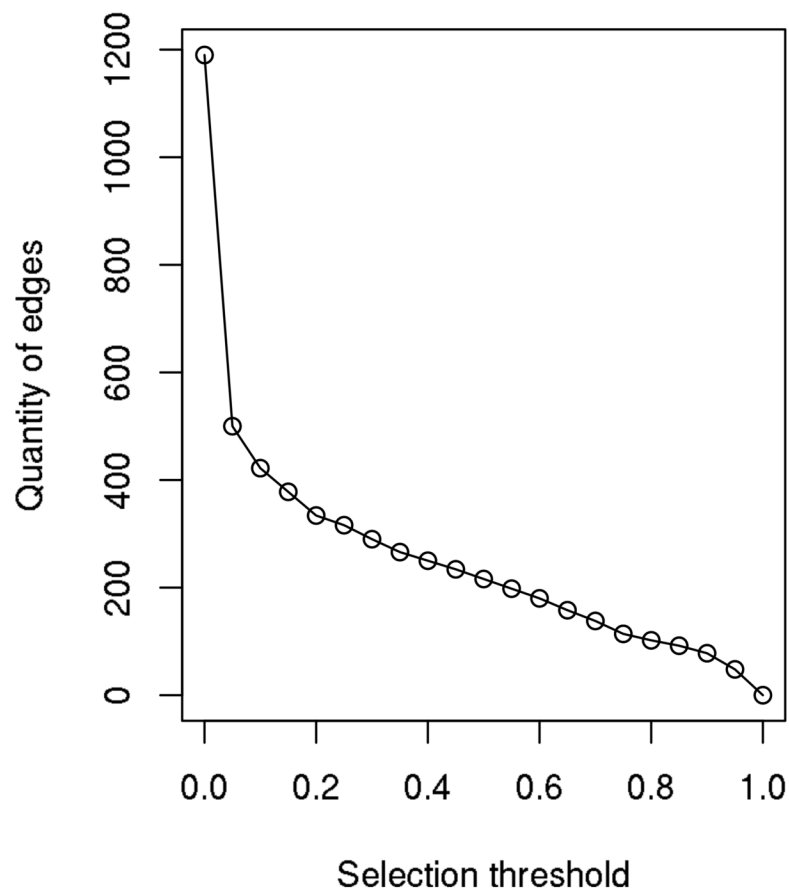


Figure S3. Quantity of selected edges for the Fall (right; n=36 species) and Spring (left; n=35 species) interaction network as a function of the selection threshold.

Table S2. Regression coefficients to explain the total number of rewirings.

	0.3 – Estimate	SE	<i>P</i> -value	0.5 – Estimate
Intercept	7.03	1.12	<0.001	4.35
Max Length	-0.003	0.01	0.71	0.01
Piscavore	-10.12	3.08	<0.01	-9.48
Max Length*Piscavore	0.05	0.02	<0.01	0.05
	Adjusted <i>R</i> ² : 0.233	Adjusted <i>R</i> ² : 0.233	Adjusted <i>R</i> ² : 0.233	Adjusted <i>R</i> ² : 0.233