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Detrimental effects of a novel flow regime on the functional trajectory of an aquatic invertebrate metacommunity

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Abstract

Novel flow regimes resulting from dam operations and overallocation of freshwater resources are an emerging consequence of global change. Yet, anticipating how freshwater biodiversity will respond to surging flow regime alteration requires overcoming two challenges in environmental flow science: shifting from local to riverscape-level understanding of biodiversity dynamics, and from static to time-varying characterizations of the flow regime. Here, we used time-series methods (wavelets and multivariate autoregressive models) to quantify flow-regime alteration and to link time-varying flow regimes to the dynamics of multiple local communities potentially connected by dispersal (i.e., a *metacommunity*). We studied the Chattahoochee River below Buford dam (Georgia, U.S.A.), and asked how flow regime alteration by a large hydropower dam may control the long-term functional trajectory of the downstream invertebrate metacommunity. We found that seasonal variation in hydropeaking synchronized temporal fluctuations in trait abundance among the flow-altered sites. Three biological trait states describing adaptation to fast flows benefitted from flow management for hydropower, but did not compensate for declines in 16 "loser" traits. Accordingly, metacommunity-wide functional diversity responded negatively to hydropeaking intensity, and stochastic simulations showed that the risk of functional diversity collapse within the next 4 years would decrease by 17% if hydropeaking was ameliorated, or by 9% if it was applied every other season. Finally, an analysis of 97 reference and 23 dam-affected river sites across the U.S. Southeast suggested that flow variation at extraneous, human-relevant scales (12-hr, 24-hr, 1-week) is relatively common in rivers affected by hydropower dams. This study advances the notion that novel flow regimes are widespread, and simplify the functional structure of riverine communities by filtering out taxa with nonadaptive traits and by spatially synchronizing their dynamics. This is relevant in the light of ongoing and future hydrologic alteration due to climate non-stationarity and the new wave of dams planned globally.

KEYWORDS

Biological traits, hydrologic alteration, invertebrates, time-series methods

1 | INTRODUCTION

Humans are changing the globe's ecosystems at an unprecedented rate (Steffen, Crutzen, & McNeill, 2007), a trend that in rivers adds to a long history of ecosystem alteration arising from water resource management, transport, flood control, and hydropower needs (Ripl, 2003). New dams are threatening some of the most biodiverse rivers worldwide (Winemiller et al., 2016; Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015; Ziv, Baran, Nam, Rodríguez-Iturbe, & Levin, 2012), and the need to increase renewable energies is also driving a new wave of damming in the developed world (Kosnik, 2010). Dams fragment rivers, alter sediment transport and geomorphology, and change the riparian and riverine habitats (Nilsson, Reidy, Dynesius, & Revenga, 2005; Poff, Olden, Merritt, & Pepin, 2007). Damming is also a primary driver of flow and temperature regime alteration (Carlisle, Wolock, & Meador, 2010; Olden & Naiman, 2010). This alteration is often manifested via dampened seasonality (due to dams muting seasonal floods), but also via new signals that arise from societal needs and thus occur at artificial timescales (e.g., "hydropeaking", or short duration discharge events emerging from variation in hydropower demand) (Bunn & Arthington, 2002; Kennedy et al., 2016). In addition to dam-induced flow alteration, climate change is increasing the frequency and magnitude of hydroclimatic extremes (Kirtman et al., 2013; Oki & Kanae, 2006), affecting river ecosystems across large regions (e.g., Ruhi, Olden, & Sabo, 2016). It is thus essential to develop quantitative toolkits that allow us to anticipate how freshwater biodiversity will respond to increasingly altered flow regimes.

Environmental variation has long been recognized as a key driver of structure and dynamics of biological communities (Chesson, 1986; Grossman, 1982; Whittaker & Goodman, 1979). Stream ecology has contributed considerably to this notion with the study of flow disturbance regimes and their effects on stream biota (Poff, 1992; Resh et al., 1988). In running waters, natural flow regimes have shaped a wide range of morphological, behavioral, and life-history adaptations of riverine and riparian organisms (Lytle & Poff, 2004; Poff et al., 1997), with seasonal high and low flows influencing physical habitat availability, longitudinal and lateral connectivity, and species diversity, functions, and interactions (Bunn & Arthington, 2002; Nilsson & Svedmark, 2002; Sabo, Finlay, Kennedy, & Post, 2010). Accordingly, the natural flow regime paradigm predicts a dependency between the persistence of native species and communities, and the preservation of the characteristic magnitudes, frequencies, durations, and timings of high and low flows (Poff et al., 1997). This prediction has been supported by many empirical studies, and has spurred abundant research on flow-ecology relationships (reviewed in Poff et al., 2010). However, most of this research has focused on static, rather than time-varying, characterizations of flow regimes (Poff, 2018). This can limit our inference when assessing ecological responses to nonstationary flow regimes, that is, flow regimes that may change over time due to climate forcing or management operations (Döll, Fiedler, & Zhang, 2009; Schneider, Laizé, Acreman, & Florke, 2013). Connecting time-varying flow regimes to riverine community dynamics is an emerging frontier for environmental flow science, and one that could help meet moving ecological targets in highly managed river ecosystems (sensu Acreman et al., 2014; Palmer et al., 2004).

The ecological impacts of flow alteration are generally observed locally, but there is an increasing recognition that local communities do not occur in a vacuum but are connected to upstream and downstream communities via dispersal (Heino et al., 2015; Tonkin et al., 2018). Although the concept of *metacommunity*, or a "set of local communities (. . .) linked by dispersal of multiple potentially interacting species" (Leibold et al., 2004) is gaining traction among freshwater ecologists, the study of metacommunities over time is still precursory (but see Erős, Sály, Takács, Specziár, & Bíró, 2012; Ruhi, Datry, & Sabo, 2017; Sarremejane et al., 2017). Research on metacommunity dynamics in the context of hydrologic alteration is important because flow variation can impair (or enhance) the source-sink dynamics that allows thriving populations and communities to subsidize declining ones (rescue effect; Gotelli, 1991). Moreover, environmental variation can have a synchronizing effect on spatially structured populations and communities, a phenomenon known as the Moran effect (Moran, 1953; Ranta, Kaitala, Lindström, & Helle, 1997). The Moran effect increases metacommunity-wide risk of collapse by weakening the Portfolio effect—the increased aggregate stability when species in a community (or local populations in a metapopulation) respond to uncorrelated sources of demographic stochasticity (Schindler, Armstrong, & Reed, 2015). In the context of flow-regime alteration, different species may present correlated temporal dynamics if they share functional adaptations that are favored (or disfavored) under the novel flow conditions. Trait-based analyses have proven powerful to understand spatial patterns of extirpations and vulnerability of stream communities in the face of hydrologic change (Kominoski et al., 2018; Pyne & Poff, 2017). Understanding trait dynamics over time may help predict how individual traits and trait combinations are likely to be lost in metacommunities affected by flow regime alteration. In turn, this may allow anticipating how resulting functional diversity—important for preserving ecological processes and services (Cadotte, Carscadden, & Mirotchnick, 2011)—may be affected.

Here, we asked whether a novel flow regime arising from flow management for hydropower could influence the long-term functional dynamics of an aquatic invertebrate metacommunity. To this end we studied a 45-km stretch of the Chattahoochee River below Buford dam (Georgia, U.S.A.), and we applied time-series techniques to long-term, daily and subdaily discharge data (1942–2015) and to long-term, spatially replicated invertebrate community data (2001–2011). In particular, we asked: (i) Is the novel flow regime induced by management for hydropower synchronizing temporal fluctuations in trait abundance across flowaltered sites? (ii) What is the metacommunity-wide effect of dam operations on individual traits and on functional diversity? and (iii) Would changing dam operations mitigate the risk of functional diversity loss?

We predicted that flow management for hydropower would filter out species with nonadaptive traits (i.e., traits favored under stable flow conditions), while selecting for traits conferring resistance against and resilience to flood disturbance (Bonada, Doledec, & Statzner, 2007). The novel, time-varying flow regime arising from seasonal variation in hydropower demand over time, combined with these differential biological responses (favored vs. disfavored traits), could potentially synchronize trait fluctuations across the metacommunity (Moran effect; see Figure 1). Therefore, local-scale, trait-level responses could scale up to region-scale functional composition and diversity, resulting in a functionally impoverished metacommunity.

2 | MATERIALS AND METHODS

Our methodological approach consists of four steps (Figure 2): (i) First, to describe the effects of Buford dam management on the downstream flow regime, we analyzed historical mean daily discharge data, and subdaily discharge data from the Chattahoochee River below Buford Dam ("Characterizing a novel flow regime"); (ii) Second, we assigned invertebrate taxa to biological traits ("Invertebrate community sampling and trait assignations"); (iii) Third, we analyzed the spatiotemporal dynamics of the aquatic invertebrate metacommunity, and investigated the effects of variation in hydropeaking intensity on individual trait state abundance and on functional diversity ("Connecting flow regime alteration to functional trajectories"); and (iv) Fourth, we simulated functional trajectories at different time horizons across a hydropeaking intensity gradient ("Anticipating the effects of hydropeaking on functional diversity"). Additionally, we conducted a large-scale analysis of flow regime alteration to test whether the patterns observed in the Chattahoochee River were representative of the U.S.- Southeast region.

2.1 | Study site

We focused on a 45-km stretch of the Chattahoochee River below Buford Dam (Georgia, U.S.A.), a federally owned dam that impounds Lake Lanier. Buford dam was completed in 1956 for hydropower and flood control purposes, has a structural height of 70 m and a storage of 3,150 cubic hectometers (USACE, 2009). The Chattahoochee River originates in the Appalachian Mountains in northern Georgia, and flows south to join the Flint River and form the Apalachicola-Chattahoochee-Flint (ACF) basin. Lake Lanier holds 63% of the total managed reservoir conservation storage in the ACF basin.

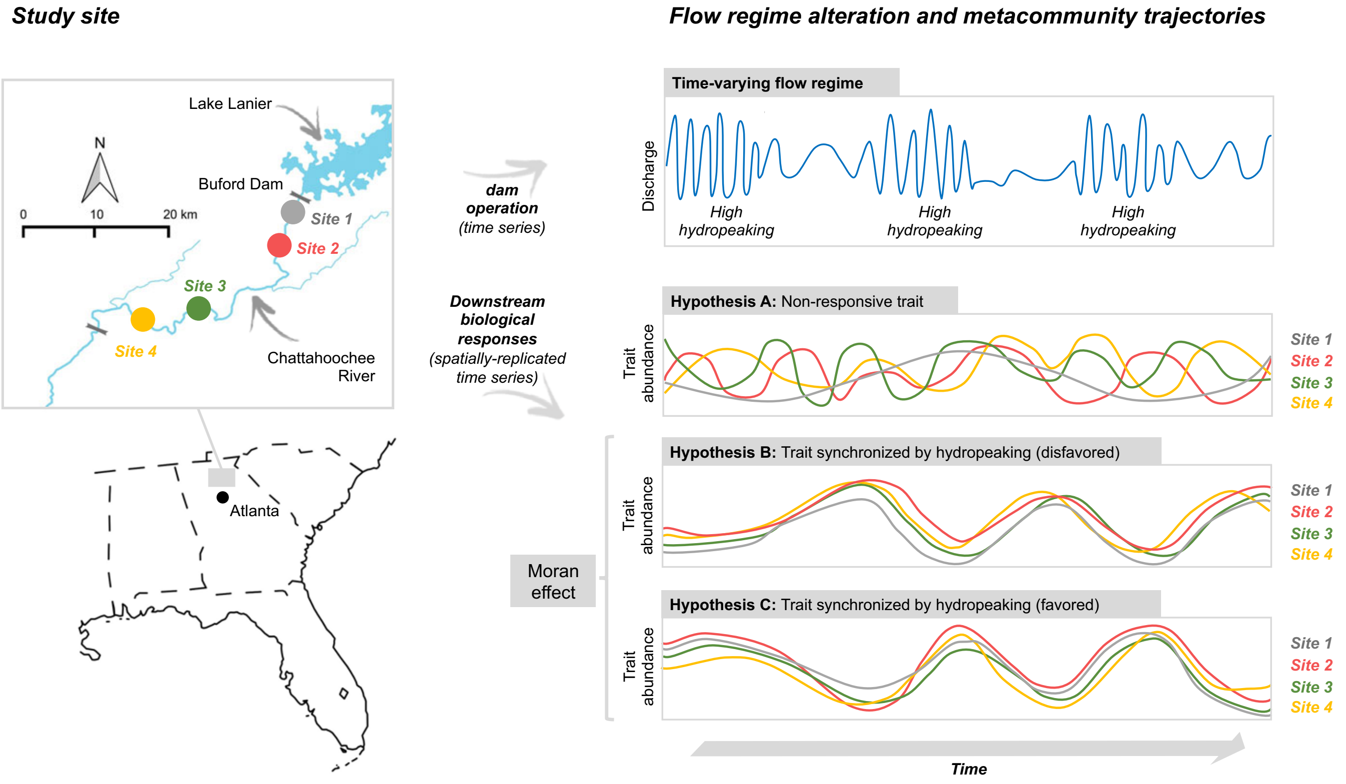


FIGURE 1 Conceptual diagram representing potential metacommunity trajectories in response to time-varying flow regime alteration. (a) If a trait state is not responsive to flow regime alteration, then it may fluctuate in an asynchronous manner across sites connected by dispersal. However, if the trait responds to flow regime alteration, then increased spatial synchrony should be expected either because the abundance of that trait decreases (b) or increases (c) with flow regime alteration (here, hydropeaking intensity) in all sites. Both (b) and (c) represent examples of the Moran effect, or an extrinsic disturbance having a synchronizing effect on a spatially structured population or community (Moran, 1953; Ranta et al., 1997). In a real metacommunity, a combination of non-responsive, disfavored, and favored traits would be expected

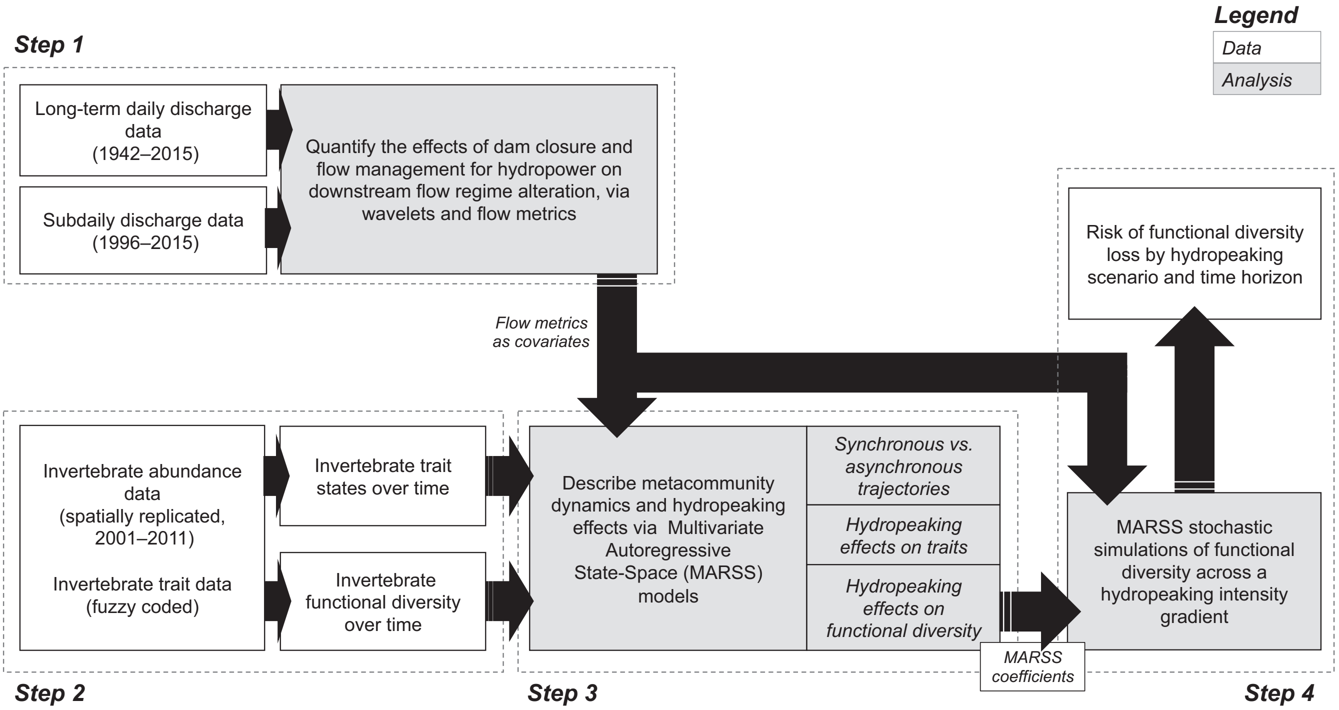


FIGURE 2 Summary of the methodological approach. Our methodological approach combines several sources of data and time-series methods, and consists of four steps: characterizing a novel, time-varying flow regime in the Chattahoochee River below Buford Dam (*step 1*); assigning biological traits to invertebrate taxa (*step 2*); analyzing the spatio-temporal dynamics of the invertebrate metacommunity, and the effects of hydropeaking intensity on individual traits and on functional diversity (*step 3*); and simulating functional trajectories across a gradient of increasing hydropeaking intensity (*step 4*). See text for details

The dam is managed to maintain a base flow of 21 m^3/s at Peachtree Creek (ca. 76 km downstream from the dam) (Holt, Pfitzer, Scalley, Caldwell, Capece et al., 2015). Moreover, the dam is operated for hydropower; accordingly, previous studies reported extreme flow variation within a single day, with diel fluctuations of >1 order of magnitude being common (Holt, Pfitzer, Scalley, Caldwell, & Batzer, 2015; Holt, Pfitzer, Scalley, Caldwell, Capece et al., 2015). Since year 2000, the National Park Service has been monitoring aquatic macroinvertebrates in four sites downstream of Buford dam, along a continuous stretch of the Chattahoochee River located 1, 8, 28, and 45 river km below the dam.

2.2 | Characterizing the novel flow regime

First, we quantified flow regime alteration using wavelets, a spectral method that allows for time-frequency decomposition of nonstationary time series (Cazelles et al., 2008; Torrence & Compo, 1998). This method allowed quantifying the effects of dam closure on flow periodicity (as in White, Schmidt, & Topping, 2005). We analyzed long-term (1942–2015) mean daily discharge data from USGS gage #02334430, located 0.5 river km downstream of Buford dam. We applied the Morlet wavelet function and red noise (temporally autocorrelated data) to determine significant wavelet power contours, using the "WAVELETCOMP" R package (Roesch & Schmidbauer, 2014). We extracted median power (normalized by variance) across the range of periods within the 1942–1956 (pre-dam) and 1957–2015 (post-dam) windows. We then applied the same procedure to instantaneous flow data from the same gage, focusing on a 20-year window (1996–2015) after dam closure. We averaged 15-min values in hourly bins and imputed missing hourly values (<1%) via linear interpolation. Peaks in wavelet power at "artificial" timescales (e.g. 24-hr) showed the effects of flow management for hydropower on the Chattahoochee flow regime.

We then sought to obtain a time series of hydropeaking intensity to use it as a predictor of the invertebrate trajectories in subsequent models. Using the instantaneous flow data set, we obtained a seasonally averaged series of maximum subdaily discharge. This measure (hereafter "hydropeaking intensity") captured the patterns of temporal variation in hydropeaking intensity observed in the wavelet, and was highly correlated ($R = .87$) with monthly net power generation at the Buford dam plant, as reported by the U.S. Energy Information Administration.

2.3 | Invertebrate community sampling and trait assignations

Every 3 months over a period of 11 years (2001–2011), aquatic macroinvertebrates were collected using Surber samplers (500-μm net) in each of the four studied sites. Three replicate samples covered each of the dominant microhabitats at the reach scale, and macroinvertebrates were preserved in 70% isopropyl and identified to the lowest possible taxonomic level (genus in most cases) in the lab (see Holt, Pfitzer, Scalley, Caldwell, & Batzer, 2015; Holt, Pfitzer, Scalley, Caldwell, Capece et al., 2015 for more details and identification keys). Abundance data from replicate samples were pooled to obtain a single sample per visit and site, and 35 taxa (after excluding taxa with <1% abundance) were retained for biological trait analyses.

We assigned taxa to traits using the U.S. EPA Freshwater Biological Traits Database, which employs as main sources Vieira et al. (2006) and Poff et al. (2006). We considered a total of 12 traits and 35 trait states describing invertebrate morphology (body size and shape, armor), behavior (mobility, dispersal mode and strength, feeding, habitat, and current preferences), and life-history strategies (voltinism, lifespan, reproductive strategies) (see Table 1). Missing trait states were filled in via existing literature (Merritt & Cummins, 1996; Tachet, Richoux, Bournaud, & Usseglio-Polatera, 2002), using family level data when genus-level data were unavailable. Although often coded as binary, trait states are generally nonmutually exclusive (Vieira et al., 2006). Thus, here we followed a fuzzy coding approach (Chevenet, Doledec, & Chessel, 1994), and the number of times that a trait state was reported for a taxa (relative to the total number of "reports" for that trait) was used to weigh the prevalence

TABLE 1 Description of traits and trait states

Trait code	Trait meaning	Trait state code	Trait state meaning
Max_body_size	Maximal body size of immatures	Large	Length >16 mm
		Medium	Length 9–16 mm
		Small	Length <9 mm
Body_shape	Body shape	Streamlined	Flat, fusiform
		Not streamlined	Cylindrical, round or bluff
Attach	Attachment	Yes	Sessile, sedentary
		No	Free-ranging
Armor	Protected by armor	None	Soft-bodied forms
		Poor	Heavily sclerotized
		Good	Protecting cases
Ovipos	Primary oviposition behavior	Free-floating	Free-floating
		On and under stones	On and under stones
		Other	Other
Feed	Primary functional feeding group	CF	Collector-filterer
		CG	Collector-gatherer
		HB	Herbivore (scraper)
		SH	Shredder
		PR	Predator (piercer, engulfer)
Habit	Primary habits	BU	Burrower
		CB	Climber
		CN	Clinger
		SP	Sprawler
		SW	Swimmer
Rheophily	Rheophily	Depo	Depositional only
		Depo_eros	Depositional and erosional
		Eros	Erosional only
Drift	Occurrence in drift	Rare	Catastrophic only
		Abund_common	Typically observed, dominant in drift samples
Voltinism	Voltinism	Bi_multivoltine	>1 Generation per year
		Univoltine	≤1 Generation per year
Adult_lifespan	Adult life span	Very short	Less than 1 week
		Short	Less than 1 month
		Long	Greater than 1 month
Adult_flying	Adult has ability to actively disperse aerially	Yes	Yes
		No	No

Traits and trait states used in this study, based on the U.S. EPA Freshwater Biological Traits Database (see text for details, and Data File S1 for the affinity matrix).

(or affinity) of that trait state. This delivered a matrix describing 35 trait state affinities × 35 taxa (Data File S1).

2.4 | Connecting flow regime alteration to invertebrate functional trajectories

We then set out to understand the dynamics of the invertebrate metacommunity, using Multivariate Autoregressive State-Space (MARSS) models with the "MARSS" R package (Holmes, Ward, & Scheuerell, 2014). MARSS models rely on theory about the patterns of temporal correlation that emerge from abiotic and biotic interactions (Ives, Dennis, Cottingham, & Carpenter, 2003), and have been used to model a wide range of ecological and conservation problems (reviewed in Hampton, Holmes et al., 2013). Because MARSS models are data-driven, they are advantageous when uncertainty around ecophysiological parameters would make the use of mechanistic models challenging. Moreover, they allow for inclusion of observation error, which is important because noise in long-term data can affect our inferences about the data (Knape & de Valpine, 2012). A MARSS model can be written in the matrix form as:

$$\boldsymbol{x}_t = \boldsymbol{B}\boldsymbol{x}_{t-1} + \boldsymbol{C}\boldsymbol{c}_{t-1} + \boldsymbol{w}_t, \quad \text{where } \boldsymbol{w}_t \sim \text{MVN}(0, \boldsymbol{Q}) \tag{1}$$

$$\boldsymbol{y}_t = \boldsymbol{Z}\boldsymbol{x}_t + \mathbf{v}_t, \quad \text{where } \mathbf{v}_t \sim \text{MVN}(0, \boldsymbol{R}) \tag{2}$$

Data enter the model as $\boldsymbol{y}$ in Equation (2) (the observation process), with $\boldsymbol{y}_t$ being observed trait state abundance across sites modeled as a function of "true" trait state abundance ($\boldsymbol{x}_t$) and $\mathbf{v}_t$, a vector of non-process (or observation) errors, with observation errors at time t being multivariate normal with mean 0 and covariance matrix $\boldsymbol{R}$. We assumed trait-specific observation error variance, and no covariance, because errors in invertebrate counts should not be correlated across sites. In the state process (Equation 1), $\boldsymbol{B}$ is an interaction matrix and can model the effect of trait state abundances on each other (in our case it was set to 'identity'). $\boldsymbol{C}$ is the matrix whose elements describe the effect of the covariate $\boldsymbol{c}_{t\text{-}1}$ (hydropeaking intensity during the precedent season) on trait state abundance at each site (hereafter *hydropeaking effects*), and $\boldsymbol{w}_t$ is a matrix of the process error, with process errors at time t being multivariate normal with mean 0 and covariance matrix $\boldsymbol{Q}$. We ran four different MARSS model structures, and one model for each trait: (i) First, we ignored the covariate, and modeled the metacommunity as a purely stochastic process. In this case we compared models not allowing for covariance in $\boldsymbol{Q}$ ("asynchronous model") to models allowing for covariance ("synchronous model"). Because here each time series is a trait state at a site, process error covariance captures spatial synchrony in the stochastic fluctuations of trait abundance. (ii) Second, we fitted two model structures including hydropeaking intensity as a covariate, comparing again synchronous to asynchronous structures in $\boldsymbol{Q}$. This aimed to show whether synchrony was driven "externally" by fluctuations in hydropeaking, and the eventual effects of hydropeaking on each trait state.

Subsequently, we fitted a model using functional diversity, instead of trait abundance, as a response (in $\boldsymbol{y}$). This allowed asking whether hydropeaking intensity controlled not only individual traits but also trait combinations. Functional diversity was measured as functional dispersion (Laliberté & Legendre, 2010), using the "FD" R package (Laliberté & Shipley, 2011). Functional dispersion represents the average distance of a sample to the functional centroid and accounts for species relative abundances. The higher the value, the larger is the trait space occupied by the species of a community, with the extirpation of functionally unique species (or functionally redundant groups of species) reducing functional dispersion and hence the mean distance of samples to the functional centroid (Laliberté & Legendre, 2010).

Trait abundance data were log-transformed, and covariate data (hydropeaking intensity) were z-scored. The support for the different model structures was assessed in an information-theoretic approach (Burnham & Anderson, 2002) using AICc. All parameters, including the ones of interest (hydropeaking effects in $\boldsymbol{C}$) were assessed via bootstrapped 95% confidence intervals.

2.5 | Anticipating the effects of hydropeaking on functional diversity

Thereafter, we simulated how alternative hydropeaking scenarios would affect the functional structure of the metacommunity. To this end, we used the parameters estimated by the MARSS functional diversity model to simulate how the metacommunity would respond to a hydropeaking gradient that spanned the range observed over the 11-year study period. We ran 5,000 stochastic simulations at each step of the hydropeaking gradient (ranging in z-scores from −1 to +1 in 0.1 steps). We then estimated the probability of observing a 90% decline in functional diversity at different time horizons, i.e., within half a year, 1, 2, and 4 years of subjecting the metacommunity to ameliorated or worsened hydropeaking scenarios. We also compared a scenario where hydropeaking was constant (i.e., present in all seasons) to a scenario where it was intermittent (i.e., season-on, season-off). This may be relevant to situations where different dams can be managed in concert to cover power demand collectively, while maximizing ecological recovery downstream of each dam.

2.6 | Southeast-wide analysis of flow regime alteration

Finally, we analyzed flow regime alteration across rivers in the U.S. Southeast region, i.e., Hydrologic Units #03 (South Atlantic-Gulf), #06 (Tennessee), and #08 (Lower Mississippi). We compared dam-affected gages with gages included in the Hydro-Climatic Data Network (HCDN), a subset of reference gages that reflect prevailing meteorological conditions and not human activities (Lins, 2012). In order to be included, dam-affected gages had to be influenced by a hydropower dam, meaning being located immediately downstream (<10% in drainage area change) of a structure classified as "Hydroelectric" either primarily or secondarily in the National Inventory of Dams (USACE, 2009). This included dams under the definition by the International Commission on Large Dams, that is, dams that were either 50 feet tall with a storage capacity of at least 5,000 acre feet, or of any height with a storage capacity of 25,000 acre feet (per the National Inventory of Dams; USACE, 2009). After assembling the list of potential HCDN and dam-affected gages, the "dataRetrieval" R package (Hirsch & De Cicco, 2015) allowed identifying gages with ≥10 years of instantaneous discharge (2007–2016). These bookends represented a trade-off between the number of gages included and the length of the time window they had in common.

We quantified flow regime alteration by focusing on differences in flow periodicity and variability between dam-affected and HCDN gages. We applied the same preprocessing procedure as for the Chattahoochee River, and excluded gages with low-quality data (>5% missing values). This delivered 23 dam-affected gages (comprising 22 dams in 16 rivers; Table 2) and 97 HCDN gages. We ran wavelets on each series, and quantified variance normalized median power at "artificial" (12-hr, 24-hr, 1-week) and "natural" timescales of flow variation (6-month, 1-year). We then focused on flow variability, computing a 10-year averaged daily coefficient of variation that has been used in the past to describe hydropeaking (Dibble, Yackulic, Kennedy, & Budy, 2015; Kennedy et al., 2016). Finally, log response ratios and associated 95% confidence showed if dam-affected and reference (HCDN) flow regimes differed in periodicity and variability.

3 | RESULTS

3.1 | Characterizing the novel flow regime

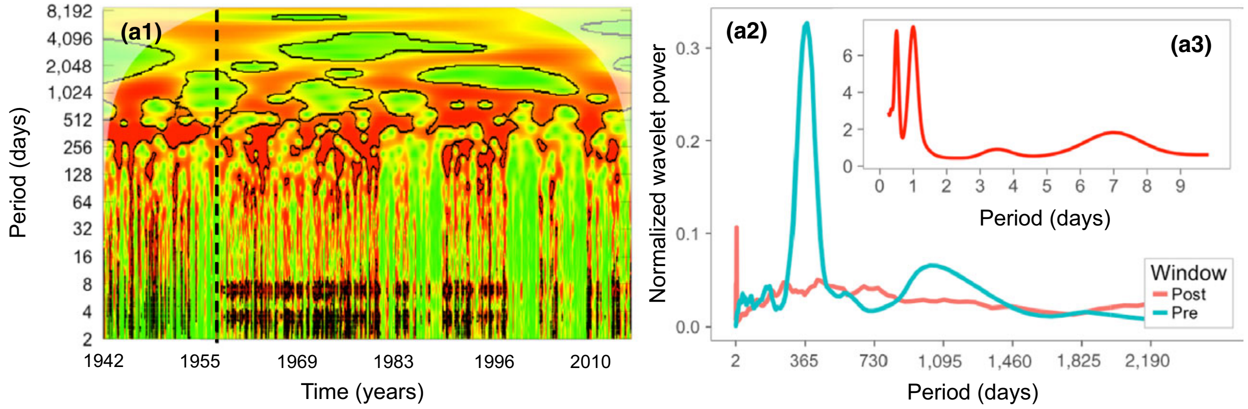
Wavelet analysis on daily discharge data showed significant effects of Buford Dam closure on downstream flow periodicity, with high-frequency signals being consistently present after dam completion in year 1956 (Figure 3a1; see vertical dashed line). When comparing pre- vs. postdam median periodicity, we found that natural flow variation at the yearly scale was lost after dam closure (Figure 3a2). Wavelet analysis on hourly discharge data showed that dam operation introduced flow variation at high frequencies, with peaks at the human relevant scales of half a day, 1 day, and 1 week (Figure 3a3). This novel flow regime arises from frequent, strong (one order of

TABLE 2 Information on the dams and gages selected for the Southeast-wide periodicity analyses (see text for selection criteria)

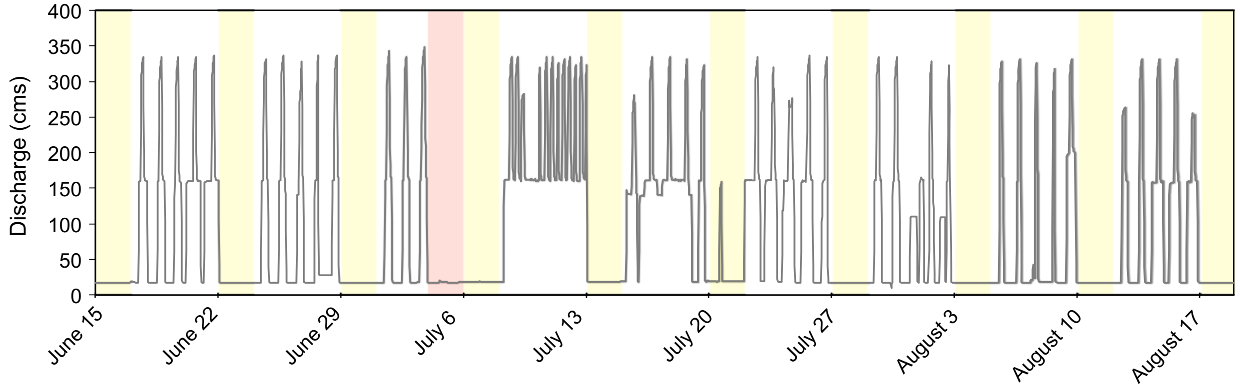
Dam name	NID_ID	Lat	Long	River	Owner	Purposes	Year	Height	Storage	USGS gage
Tallassee Shoals	GA83013	33.9899	−83.5007	Middle Oconee River	P	H	1986	48	500	02217500
Sinclair	GA00836	33.1405	−83.2018	Oconee River	PU	H,WS,R	1953	105	490,000	02223000
Buford	GA00824	34.1600	−84.0733	Chattahoochee River	F	H,FC,R	1956	231	2,554,000	02334430
Morgan Falls	GA00842	33.9681	−84.3841	Chattahoochee River	PU	H,WS,R	1903	65	3,150	02336000
Morgan Falls	GA00842	33.9681	−84.3841	Chattahoochee River	PU	H,WS,R	1903	65	3,150	02335815
Jim Woodruff	FL00435	30.7083	−84.8649	Apalachicola River	F	H,FC,N,R	1952	92	406,200	02358000
West Point	GA00820	32.9183	−85.1883	Chattahoochee River	F	H,FC,R	1974	121	605,000	02339500
Flint River	GA00835	31.6026	−84.1370	Flint River	PU	H	1921	60	37,000	02352500
Niagara	VA16101	37.2549	−79.8750	Roanoke River	PU	H	1906	60	425	02056000
Smith River	VA08913	36.6650	−79.8833	Smith River	LG	H	1904	38	2,600	02073000
Philpott	VA08901	36.7833	−80.0283	Smith River	F	H,WS,R,FW,O	1953	220	318,300	02072000
Riverside	VA14307	36.5950	−79.3966	Dan River	P	H,R	1870	10	700	02075045
Emporia	VA08101	36.6963	−77.5585	Meherrin River	LG	H,WS,FW	1908	43	3,800	02052000
Lake Robinson	SC00632	34.4016	−80.1516	Black Creek	PU	H	1960	55	55,500	02130910
Blewett Falls	NC00494	34.9880	−79.8798	Pee Dee River	PU	H,WS,R	1912	77	97,000	02129000
Parr Shoals	SC01069	34.2610	−81.3321	Broad River	PU	H	1914	55	32,000	02161000
Wateree	SC00485	34.3367	−80.7015	Catawba River	P	H,WS	1919	92	262,394	02148000
Saluda Lake	SC00024	34.8516	−82.4850	Saluda River	PU	H	1905	59	7,519	02162500
Piedmont	SC01068	34.7014	−82.4625	Saluda River	P	H	1874	26	300	02163001
Buzzards Roost	SC00109	34.1692	−81.9025	Saluda River	LG	H,R	1940	82	256,000	02166501
Roanoke Rapids	NC00827	36.4817	−77.6733	Roanoke River	PU	H,WS,R,FW	1955	72	80,690	02080500
Remmel	AR00535	34.4272	−92.8939	Ouachita River	PU	H,R,FW,O	1925	75	57,260	07359002
Ivy River	NC83017	35.7718	−82.6190	Ivy River	P	H	1918	63	40	03453000

Dam name = Official name of the dam; NID_ID = Official National Inventory of Dams (NID) identification number; Lat = Latitude at dam centerline, in decimal degrees, NAD83; Long = Longitude at dam centerline, in decimal degrees, NAD83; River = River or Stream designation; Owner = type of owner [F, Federal; LG, Local Government; P, Private; PU, Public Utility]; Purposes = primary and secondary purposes [H, Hydroelectric; FW, Fish and Wildlife Pond; FC, Flood Control; N, Navigation; R, Recreation; WS, Water supply; O, Other]; Year = Year when the original main dam structure was completed; Height = Height of the dam (in feet); Storage = Storage of the dam (in acre-feet); USGS gage = code of the streamgaging station paired with this dam. See (USACE, 2009) and (Goteti & Stachelek, 2016) for more detailed definitions.

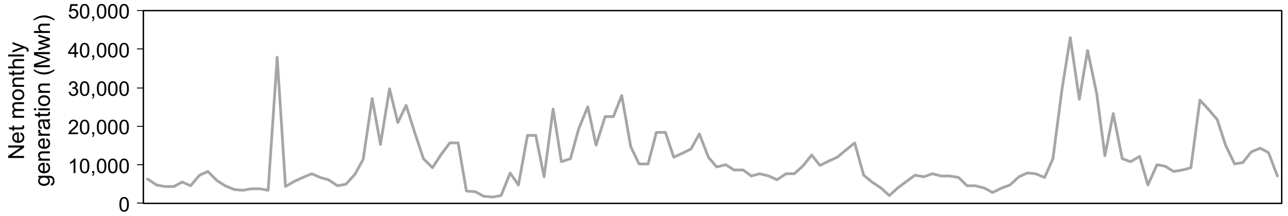
(a) Wavelet analysis



(b) High hydropeaking intensity discharge series sample



(c) Hydropower generation



(d) Hydropeaking intensity

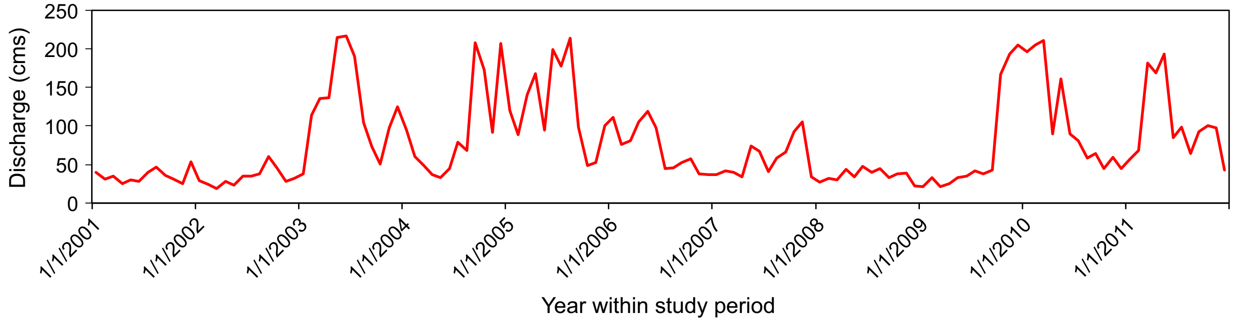


FIGURE 3 Characterization of Chattahoochee River's novel flow regime. (a) Wavelets on daily and subdaily discharge data. (a1) Wavelet on daily discharge data (1942–2015). The vertical dashed line marks dam completion. (a2) Median wavelet power for the pre-dam (1942–1956) vs. post-dam time window (1957–2015). (a3) Median wavelet power within the post-dam period (1996–2015), obtained on hourly discharge data. (b) Sample of the hourly discharge time series in the Chattahoochee River downstream of Buford Dam, during a period of high hydropeaking intensity (June 15, 2013 to August 19, 2013). Note most weeks present five discharge peaks (one per day between Monday and Friday), with no releases in weekends (highlighted in yellow). The third analyzed week comprised the 4th of July (a Thursday), highlighted in red. (c) Time series of monthly net hydropower generation at the Buford dam plant, as reported by the U.S. Energy Information Administration (https://www.eia.gov/electricity/data/browser/#/plant/759). (d) Fluctuations in hydropeaking intensity over time, measured as the average magnitude of maximum subdaily discharge events

magnitude) discharge releases occurring once or twice a day, often Monday to Friday (Figure 3b). These subdaily high-flow releases respond to peak electricity demand, and can be absent during weekends and vacation days (Figure 3b). Subdaily high flows represent the magnitude of hydropeaking events, and a monthly average of this metric over the study period (2001–2011) was highly correlated (R = .87) with monthly hydropower production at the Buford Dam plant (Figure 3c,d). Hydropeaking intensity fluctuated over the study period, with periods of relatively low alteration by hydropeaking being punctuated by intervals of high hydropeaking alteration (e.g., in years 2003, 2005, 2010, 2011) (Figure 3d).

3.2 | Flow regime alteration and functional trajectories of the metacommunity

The comparison of MARSS model structures showed that when not considering any covariate, synchronous dynamics across sites were better supported (Table 3). The same was true for models considering hydropeaking intensity as a covariate; however, smaller AICc values in 10 out of the 12 models indicated that the evidence for synchronous dynamics decreased after including hydropeaking intensity as a covariate (Table 3). This suggested that part of the temporal variability in trait abundance within and across sites was driven by variation in hydropeaking. This observation was corroborated by comparing the estimated parameter values of process error variance and covariance: the inclusion of hydropeaking intensity as a covariate in the models decreased the magnitude of process error variance (**Q** diagonal values in Equation 1), process error covariance (**Q** off-diagonal values in Equation 1), and their ratios (i.e., covariance normalized by variance, or correlation) across models (Figure 4a–c). Moreover, trait states responding more strongly to hydropeaking intensity (in either direction) decreased more in covariance when including hydropeaking intensity as a covariate (Figure 4d). This indicates that hydropeaking intensity affected some, but all not trait states, with sensitive traits being spatially synchronized by this exogenous influence. Hydropeaking had significantly negative effects on 16 trait states and significantly positive effects on three trait states, whereas 16 trait states did not respond significantly (Figure 5a). The three trait states that benefitted from hydropeaking were filterer, erosional, and clinger strategies (Figure 5a). In turn, most trait states negatively affected by hydropeaking reflected morphological, behavioral, and life-history adaptations to environmental stability (e.g., long lifespans, univoltinism, large body sizes, use of depositional habitats; Figure 5a).

Finally, in order to determine how these trait-specific effects scaled up in terms of functional diversity at the metacommunity level, we fitted an analogous MARSS model on functional diversity. This showed a negative effect of hydropeaking on functional diversity—stronger than any of the individual trait responses (Figure 5b). This significant relationship served as a basis for simulating the effects of alternative hydropeaking scenarios on invertebrate functional diversity.

3.3 | Anticipating the effects of hydropeaking on functional diversity

The MARSS stochastic simulations run across a gradient of hydropeaking intensity showed that the risk of functional diversity collapse (i.e., the probability that functional diversity would decrease by at least 90% within the forecasted period) increased with hydropeaking intensity

TABLE 3 Support for MARSS model structures considering asynchronous vs. synchronous metacommunity dynamics

	MARSS model structure without covariate			MARSS model structure with covariate		
	Asynchronous	Synchronous	ΔAICc	Asynchronous	Synchronous	ΔAICc
Trait						
Body size	1502.4	1467.5	34.9	1494.8	1464.4	30.4
Body shape	1094.2	1075.0	19.2	1085.4	1070.5	14.9
Attached	1066.7	1056.6	10.1	1061.8	1053.9	7.9
Armor	1070.5	1066.6	3.9	1068.5	1066.4	2.1
Oviposition	1613.1	1603.8	9.3	1616.4	1606.8	9.6
Feeding	2250.1	2206.0	44.1	2234.9	2207.1	27.8
Habit	2266.0	2217.0	49.0	2242.2	2208.5	33.7
Rheophily	1590.5	1549.3	41.2	1565.8	1537.8	28.0
Drift	1058.4	1052.1	6.3	1059.7	1052.9	6.8
Voltinism	1085.7	1061.6	24.1	1081.5	1059.7	21.8
Adult lifespan	1605.2	1590.2	15.0	1599.2	1586.1	13.1
Adult flying	1105.5	1086.9	18.6	1095.9	1080.0	15.9

The "Synchronous" model structure allows for process error covariance within trait states (across sites), whereas the "Asynchronous" model structure sets to zero all off-diagonals in the process error variance-covariance (**Q**, see Equation 1 in Methods). On the left, models without a covariate (i.e., making no assumption of what is driving coordinated and uncoordinated fluctuations in trait abundance over time). On the right, models with a covariate (i.e., including hydropeaking intensity effects). Models including process error covariance and hydropeaking intensity as a covariate were generally better supported. One MARSS model was fit for each trait, modeling trait state abundance across sites as a response. Values are Akaike Information Criteria corrected for small sample size (AICc).

(Figure 6a). Change in risk tended to accumulate over time. This way, ameliorating hydropeaking intensity (from average to low) for half a year would only slightly decrease the functional collapse risk (by 2.0%). However, this influence would grow if hydropeaking was ameliorated for a year (5.8% decrease), 2 years (10.0% decrease), or 4 years (17.0% decrease) (Figure 6a). On the flip side, the detrimental effects of increasing hydropeaking intensity (from average to high) on functional collapse risk also accumulated over time, from a 3.3% increase in risk within a semester to a 6.8%, 12.7%, and 16.3% increase after 1, 2, and 4 years respectively (Figure 6a). The entire hydropeaking gradient used for the simulations (i.e., z-scores ranging from −1 to +1) was observed during the study period. Thus, these simulations are relevant to the range of flow regimes experienced by the metacommunity, and show that regardless of stochasticity in its dynamics, ameliorating hydropeaking intensity would have desirable effects on the risk of functional diversity loss.

If an intermittent (i.e., season-on, season-off) rather than a constant hydropeaking scheme were applied, risk would decrease even further (Figure 6b). Average hydropeaking intensities applied intermittently could decrease functional collapse risk by 1.3%–9.1%, and increased hydropeaking intensities applied intermittently would have only negligible effects (−0.5% to +1.0% change in risk) (Figure 6b).

3.4 | Southeast-wide analysis of flow regime alteration

Finally, we quantified the extent of flow regime alteration by hydropower dams across the U.S. Southeast climatic region, by comparing flow periodicity and variability between dam-affected and reference (HCDN) gages. The comparison of wavelet power at the five targeted periods (12-hr, 24-hr, 1-week, 6-month, 1-year) showed that "artificial" flow cycles are relatively more prevalent in dam-affected reaches, but "natural" flow cycles are equally present in dam-affected and unaffected sites (Figure 7a). Additionally, flow variability in dam-affected rivers was more than twice that of reference rivers (Figure 7b). These results suggest that water storage by hydropower dams does not always dampen the natural scales of flow variation (6-month, 1-year). However, flow management for hydropower does consistently introduce artificial signals (subdaily, daily, and weekly flow cycles) that increase variation in downstream flow regimes.

4 | DISCUSSION

Global installed hydropower capacity is projected to double over the next 20 years (Zarfl et al., 2015), creating an increasing need to anticipate the impacts of high-head storage hydropower plants on downstream biodiversity. Two standing challenges in environmental flow science are shifting from static to dynamic (time-varying) characterizations of flow regimes, and from local to riverscape-level responses of population rates and species traits (Poff, 2018). Here, we used a quantitative approach based on multivariate time-series models to connect a timevarying, novel flow regime to the temporal dynamics of an invertebrate metacommunity. We found that long-term variation in hydropeaking intensity controlled the dynamics of

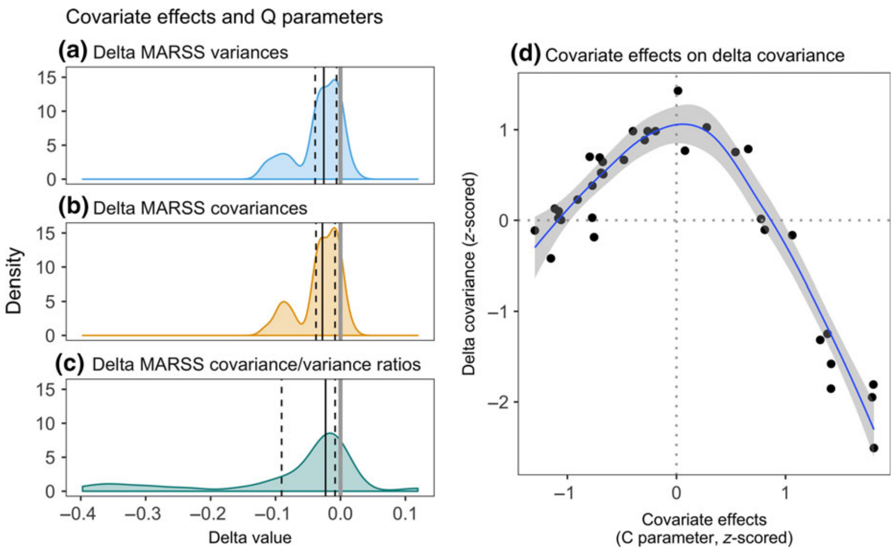


FIGURE 4 Covariate effects and Q parameters. We compared MARSS models with and without a covariate, focusing on how estimated process error variance and covariance values changed with the inclusion of the covariate (hydropeaking intensity) (see ***Q*** and ***C*** in Methods, Equation 1). (a) Density plot of delta variances (i.e., the difference in trait state-specific process error variance estimated by models with and without hydropeaking intensity as a covariate). (b) Density plot of delta covariances (i.e., the difference in trait state-specific process error covariance estimated by models with and without hydropeaking intensity as a covariate). (c) Density plot of delta correlation (i.e., the difference in trait state-specific process error covariance-variance ratios estimated by models with and without hydropeaking intensity as a covariate). (d) Trait states responding more strongly to hydropeaking intensity (in either direction) decreased more in covariance when including hydropeaking intensity as a covariate, showing that hydropeaking explains spatial synchrony in some but not all trait states. Each point is a trait state, and the relationship was smoothed via LOESS

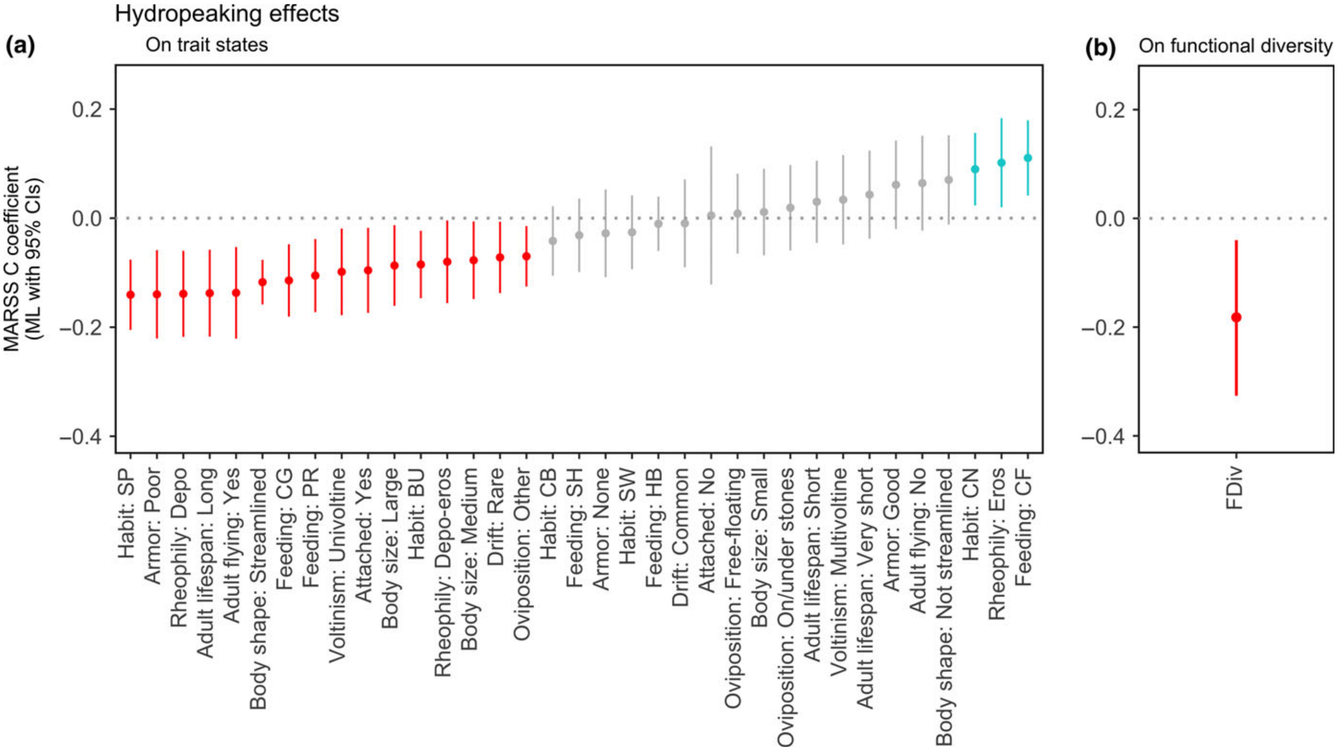


FIGURE 5 Hydropeaking effects on individual trait states. (a) MARSS models were run independently on each trait, modeling trait states at each site as a function of hydropeaking intensity. This figure collates all hydropeaking effects across models. The bootstrapped *C* coefficient represents the effect size of hydropeaking effects: in red, trait states negatively affected by hydropeaking; in green, those positively affected; in gray, those not significantly affected (confidence intervals overlapping with zero). See trait state codes in Table 1. (b) Hydropeaking effects on functional diversity (measured as functional dispersion), as estimated by the MARSS functional diversity model

downstream invertebrates by filtering out some nonadaptive traits (i.e., traits favored under stable flow conditions). Because these responses were consistent across sites, seasonal variation in hydropeaking intensity increased spatial synchrony in trait composition across the modeled river section (Moran effect; Figure 1). Hydropeaking had strong, negative effects on metacommunity-wide functional diversity. The risk of near-term functional collapse (i.e., the probability of hitting a 90% decline threshold in functional diversity within the next 4 years) could be partially mitigated if hydropeaking was ameliorated or applied every other season. These results advance the notion that novel flow regimes can influence the long-term dynamics of downstream metacommunities and simplify their functional structure.

4.1 | Trait responses to hydropeaking

One of the artificial signals introduced by hydropower dams is hydropeaking: frequent, short duration discharge events arising from fluctuation in the demand for hydroelectric power. Abundant research has shown how diel, rapid water-level rise and recession cycles can reduce biomass, abundance, and diversity of aquatic fauna via stranding, displacement, thermal stress, and recruitment limitation (e.g., Kennedy et al., 2016; Liebig, Cereghino, Lim, Belaud, & Lek, 1999; Moog, 1993; Valentin, Wasson, & Philippe, 1995). In our case, more than half of the traits responded significantly to hydropeaking, most of them negatively. As expected, several traits favored under stable, lentic environments responded negatively to hydropeaking, whereas the opposite was true for some traits conferring resilience and resistance strategies to frequent flood disturbance (Bonada et al., 2007).

We observed a high redundancy within "winner" and "loser" traits. For example, 86% of the rheophilic species (i.e., taxa with high affinities for erosional [fast-flow] habitats) were also collector-filterers, and 71% had both rheophilic and clinger habits (Data File S1)—the three strategies that benefited the most from hydropeaking (Figure 5a). Conversely, taxa negatively affected by hydropeaking were mainly collector-gatherer depositional midges; or larger taxa with longer life cycles (i.e., long-lived, univoltine species). Trait redundancy was again high—for instance, all large invertebrates were long-lived; and 75% of predators (or 71% of collector-gatherers) were depositional or partly depositional taxa (Data File S1). Functional redundancy can increase resilience in a metacommunity by making it more difficult for a trait to become extirpated (Angeler et al., 2016). However, that requires response diversity by traits to be high: different species need to respond in diverse directions to disturbance to "insure" the range of traits. This was not the case in our study, as most traits responded negatively to hydropeaking. This suggests a weakened capacity of the metacommunity to respond to disturbance (Angeler & Allen, 2016), which is consistent with

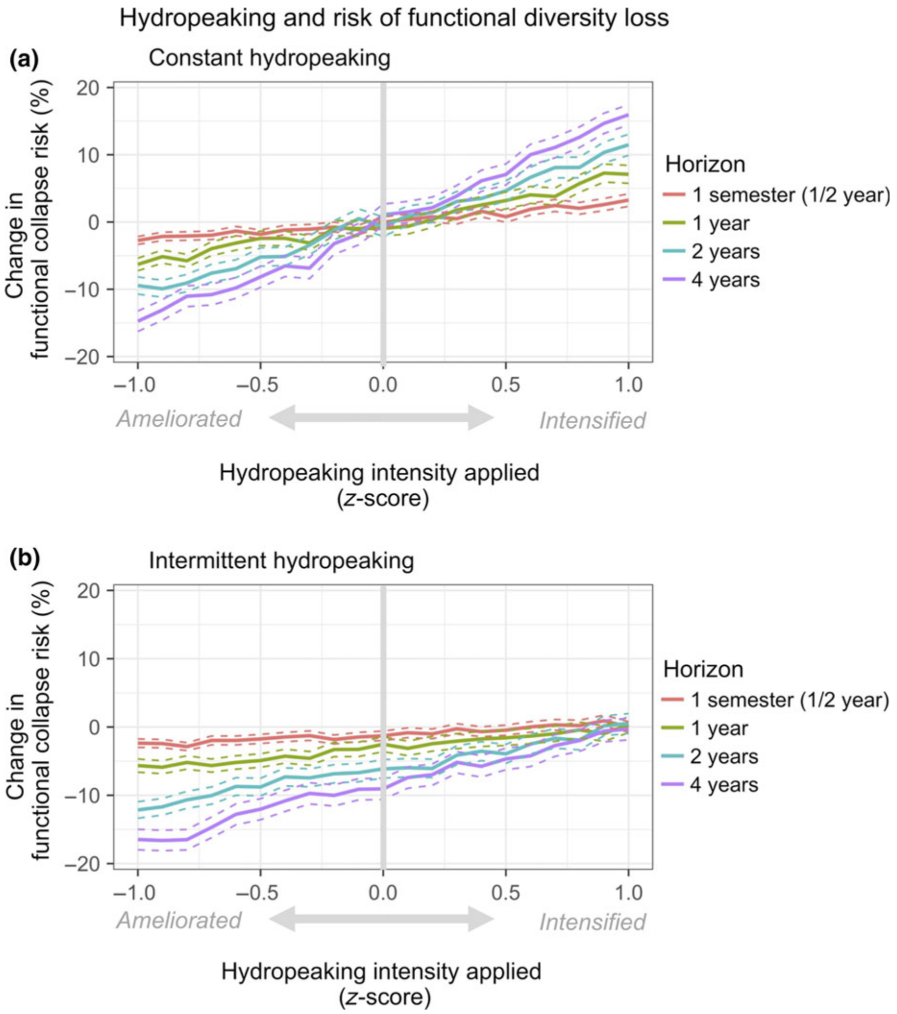


FIGURE 6 Effects of hydropeaking on risk of functional diversity collapse. The risk of hitting a critical (90%) decline threshold in functional diversity was simulated via MARSS stochastic realizations across a gradient of hydropeaking intensity and at four different time horizons (half a year, 1, 2, 4 years). (a) Constant hydropeaking strategy, (b) intermittent hydropeaking strategy (i.e., season-on, season-off). The solid lines represent mean change in risk (i.e., estimated risk at a given hydropeaking level relative to basal risk), dashed lines represent standard errors. See text for details

functional diversity responding stronger to hydropeaking than any of the individual traits (Figure 5b). This emergent property is likely generalizable in metacommunities consisting of highly redundant species (i.e., species with limited combinations of trait states) that respond similarly to disturbance.

4.2 | Functional collapse risk and the Moran effect

The model comparison showed that synchronous trajectories were better supported than asynchronous ones, and that hydropeaking intensity explained this spatial covariation in 10 of the 12 trait-specific models. Asynchronous dynamics increase metapopulation stability, because when local populations have independent dynamics from each other, thriving populations can rescue those impacted by local-scale shocks. Similarly, species-richer communities generally deliver more stable services, as different species may respond to uncorrelated sources of demographic stochasticity (Schindler et al., 2015). Such variance dampening in a structured metacommunity is often referred to as the portfolio effect, a concept borrowed from financial markets, where asset diversity stabilizes financial portfolios (Markowitz, 1991). In our study, however, the portfolio effect—and the resulting cross-scale resilience (Angeler & Allen, 2016)—was weakened because suites of traits responded to hydropeaking in a coordinated manner across sites. This observation can be explained by the Moran theorem, which poses that the temporal correlation of two populations is a function of the correlation between the environmental regimes in which they live (Moran, 1953; Ranta et al., 1997). The Moran effect has often been studied across large spatial scales (e.g., to study ecological responses to climate forcing; Stenseth et al., 2002). Here, we propose it may also play a role in human-altered riverscapes, for example when large dams affect long river sections (like in this study), or when cascades of smaller dams operate simultaneously. Taxa drifting and flying from tributaries may be able to rescue declining functional guilds in regulated main stems (Sabo et al., 2018). However, when no nearby propagule sources exist (e.g., in headwater dams, or in highly dammed river basins) the Moran effect may increase the effective risk of functional collapse. Many individual traits are linked to species' functional roles in ecosystems, e.g., feeding strategies are linked to organic matter processing (Graça, 2001); and voltinism, flying, and drift are linked to terrestrial and in-stream subsidies (Baxter, Fausch, & Carl Saunders, 2005; Uno & Power, 2015). Additionally, multifunctionality (i.e., trait richness, and diversity of trait

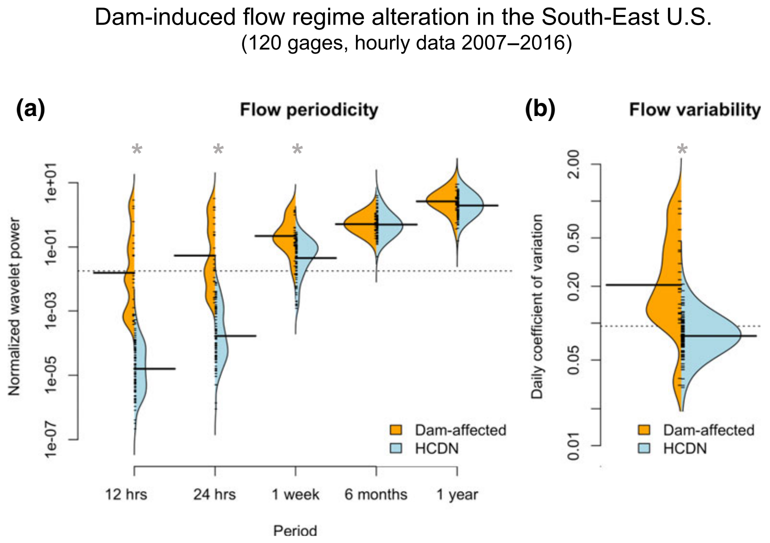


FIGURE 7 Effects of dam-induced flow regime alteration in the U.S. Southeast. Analysis of flow periodicity and variability across the South Atlantic-Gulf, Tennessee, and Lower Mississippi Hydrologic Units (23 dam-affected gages, 97 HCDN gages). (a) Median flow periodicity, measured by wavelets run on a 10-year window (2007–2016) of hourly discharge. (b) Daily coefficient of variation averaged over the 10-year window. HCDN are reference gages included in the USGS Hydro-Climatic Data Network (Lins, 2012). Horizontal black lines represent group and overall means; asterisks show significant differences measured by log response ratios (Figure S3)

combinations across community members) is positively associated with the maintenance of ecosystem processes and services (Cadotte et al., 2011). Therefore, flow regime alteration may impair ecosystem function not only locally but across river sections, increasing the riverscape-level risk of functional collapse via the Moran effect.

4.3 | Periodicity alteration as an emerging consequence of global change

Predictable (seasonal) signals, and stochastic (aseasonal) environmental noise, both control the structure and dynamics of aquatic biota across levels of biological organization (Grossman, 1982; Sabo et al., 2010). Periodicity is an important feature of flow regimes, and influences river biodiversity and productivity (Bunn & Arthington, 2002; Jardine et al., 2015). The anthropogenic alteration of environmental periodicity (or "periodicity syndrome") we found in the study system and regionally (Figures 3a and 7a) represents a shift in flow predictability across the frequency domain, toward the human-relevant, short timescales of variation. Periodic variation is, in theory, a more benign type of environmental variation than stochastic variation—for it is predictable and organisms can cope with predictable variation via increased tolerance to stress (Resh et al., 1988; Sabo & Post, 2008). However, periodicity at the half-daily, daily, and weekly scales may not be coupled to life-history adaptations of aquatic or riparian organisms (Lytle & Poff, 2004). Rapid evolution in response to novel habitat conditions can occur within only a few generations (Hendry, Wenburg, Bentzen, Volk, & Quinn, 2000), and high-frequency flow cycles have certainly impacted short-lived riverine organisms for decades (40% of the U.S. hydroelectric dams were completed before 1920; Goteti & Stachelek, 2016; USACE, 2009). Although no adaptations to altered flow regimes have been reported so far, periodicity syndromes—as a form of extreme change in background environmental fluctuations—could be shaping adaptations of riverine biota through phenotypic plasticity and subsequent genetic assimilation (Lande, 2009; Thompson, 1998).

Here, we focused on periodicity syndromes in flow regimes, but similar alteration has been reported in light cycles (due to artificial lighting and skyglow; Gaston, Duffy, Gaston, Bennie, & Davies, 2014) and in sound cycles (due to artificial background noise; Pijanowski et al., 2011; Warren, Katti, Ermann, & Brazel, 2006). The spectral methods we used offer a way to study changes in environmental periodicity regardless of their nature. Wavelets are being quickly adopted by ecologists (Carey, Hanson, Lathrop, & Amand, 2016; Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017; White et al., 2005), and hold particular promise in environmental flow science because they are free from the assumption of stationarity (Cazelles et al., 2008). Given the growing availability of environmental time series (Hampton, Strasser et al., 2013), the combination of time-series methods in the frequency and time domains (e.g., Grossman & Sabo, 2010; Ruhi, Holmes, Rinne, & Sabo, 2015) will offer increasing opportunities to anticipate the effects of altered periodic and stochastic environmental variation on ecological communities.

5 | CONCLUDING REMARKS

This study adds to growing evidence that novel flow regimes can be detrimental to river ecosystem structure and functioning (e.g., Cross et al., 2013; Kennedy et al., 2016; Tonkin, Merritt, Olden, Reynolds, & Lytle, 2017)—in this case, by influencing the functional dynamics of the downstream invertebrate metacommunity. Our finding on the synchronizing effect of hydropeaking underscores the need to understand biodiversity responses to flow alteration over space *and* time (Angeler & Allen, 2016; Poff, 2018). In turn, the observed relationship between hydropeaking and functional diversity decline risk may help inform dam management strategies that balance ecological outcomes with socio-economic goods (Poff et al., 2016; Sabo et al., 2017). Trends in streamflow regulation and hydroclimatic change are accelerating (IPCC, 2014; Zarfl et al., 2015), and restoring reference (predam) flow regimes is often unfeasible (Acreman et al., 2014). Thus, a better understanding of the consequences of the different facets of novel flow regimes may increase the efficacy of environmental flow design in the face of global change.

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