

Anomalous droughts, not invasion, decrease persistence of native fishes in a desert river

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Abstract

Changing climate extremes and invasion by non-native species are two of the most prominent threats to native faunas. Predicting the relationships between global change and native faunas requires a quantitative toolkit that effectively links the timing and magnitude of extreme events to variation in species abundances. Here, we examine how discharge anomalies – unexpected floods and droughts – determine covariation in abundance of native and non-native fish species in a highly variable desert river in Arizona. We quantified stochastic variation in discharge using Fourier analyses on >15 000 daily observations. We subsequently coupled maximum annual spectral anomalies with a 15-year time series of fish abundances (1994–2008), using Multivariate Autoregressive State-Space (MARSS) models. Abiotic drivers (discharge anomalies) were paramount in determining long-term fish abundances, whereas biotic drivers (species interactions) played only a secondary role. As predicted, anomalous droughts reduced the abundances of native species, while floods increased them. However, in contrast to previous studies, we observed that the non-native assemblage was surprisingly unresponsive to extreme events. Biological trait analyses showed that functional uniqueness was higher in native than in non-native fishes. We also found that discharge anomalies influenced diversity patterns at the meta-community level, with nestedness increasing after anomalous droughts due to the differential impairment of native species. Overall, our results advance the notion that discharge variation is key in determining community trajectories in the long term, predicting the persistence of native fauna even in the face of invasion. We suggest this variation, rather than biotic interactions, may commonly underlie covariation between native and non-native faunas, especially in highly variable environments. If droughts become increasingly severe due to climate change, and floods increasingly muted due to regulation, fish assemblages in desert rivers may become taxonomically and functionally impoverished and dominated by non-native taxa.

Keywords: ecohydrology, environmental variation, global change, MARSS, stream fish, time-series analyses

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Introduction

River ecosystems comprising ~65% of global discharge have moderate to high water scarcity (Vörösmarty *et al.*, 2010) and water scarcity has been implicated with lower native and higher non-native freshwater species richness (Sabo *et al.*, 2010a). In the Southwest United States, an ongoing transition to a more arid climate (Seager *et al.*, 2007) interacts with an increasing human appropriation of streamflow (Sabo *et al.*, 2010a) to influence mean annual streamflow and discharge variation. As a result, even large and highly regulated watercourses like the Colorado River are drying with increasing frequency (Gleick, 2003). Prolonged droughts and ‘lentification’ (i.e., the transformation of the habitat

character of rivers in the direction from lotic to lentic; Sabater, 2008) will likely continue to impact river structure and functioning across broad geographic scales. Furthermore, the increasing intensification of the global hydrological cycle is expected to cause a higher frequency of extreme events of both signs (i.e., droughts and floods) in the Northern hemisphere’s subtropics like the US sunbelt (Oki & Kanae, 2006; Kirtman *et al.*, 2013). Mounting evidence suggests that climate change impact studies, by focusing on changes in climate means rather than on variability, may underestimate the full impacts of climate change (Easterling *et al.*, 2000; Thornton *et al.*, 2014). Therefore, it is crucial to develop and apply statistical tools that allow us to quantify the response of ecological communities to environmental variation and project how these responses will change under new regimes characterized by increased variation.

The relative importance of discharge variation and species interactions in determining fish community

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composition and structure (i.e., relative abundances) has been a long standing topic of study, precipitating numerous lively debates (Grossman, 1982; Rahel *et al.*, 1984; Grossman *et al.*, 1985; Moyle & Vondracek, 1985). These early studies explored the notion that community trajectories were either predictable by virtue of consistent species interactions, or unpredictable by virtue of stochastic variation in flow. Support was found for both hypotheses, and recent work has shown how this false dichotomy can be resolved by considering communities to be increasingly driven by discharge variation as the stochastic component of environmental variation increases (Grossman & Sabo, 2010). Environmental variation is now widely accepted as a predictable driver of ecological processes across a wide range of organization levels and ecosystem types (e.g., Stacey & Taper, 1992; Sæther, 1997; Sabo *et al.*, 2010b) and it is accordingly considered central to eco-evolutionary theory (Lytle, 2001; Ruokolainen *et al.*, 2009). Here, we explore the role of discharge variation as a predictor of community structure within the context of climate extremes and species invasions—two of the most poignant signals of global change. Specifically, we develop a new set of integrated tools to project the potential impacts of different regimes of environmental variation under long-term environmental change on the success of invasion and the resilience of native faunas.

Parsing out the relative importance of biotic vs. abiotic interactions in determining long-term community trajectories would improve theories of invasive species' control (Mack *et al.*, 2000; Sabo, 2005). In aridland riparian ecosystems, hydrological alterations induce dominance shifts in plant communities from native to introduced species (Stromberg *et al.*, 2007a). Native floras do not decline because of invasion, but rather as a direct result of the same environmental conditions that favor introduced species. Abundant literature revolving around the 'natural flow regime' concept (Poff *et al.*, 1997; Lytle & Poff, 2004) has similarly described differential (and generally opposite) effects of altered flow regimes on native compared to non-native fishes. This pattern was described long ago by Seegrist & Gard (1972) and since then an increasing body of evidence has supported the notion that the loss of natural flow regimes favors the non-native assemblage and decimates the native one (e.g., Bernardo *et al.*, 2003; Propst *et al.*, 2008; Gido & Propst, 2012; Mims & Olden, 2013; Pool & Olden, 2014). The early work of Seegrist & Gard (1972) advanced the notion that antagonistic interactions between non-native and native species is enhanced by flow regime alteration; however, analytical limitations have prevented explicit quantification of the relative strength of biotic (species interactions) and abiotic (flow) effects on native species. Here, we

address this by using a novel combination of time-series methods to ask whether negative covariation between flow changes and native fish abundances is a direct consequence of flow changes (abiotic paradigm), or of flow-mediated changes in non-native species abundances (biotic paradigm). In streams where native species resilience is determined by interactions between non-native and native species, the restoration of the native community would require mechanical removal of non-native faunas. By contrast, flow manipulations would be the best recourse where changes to the natural flow regime underlie declines in native species. The suitability of these management strategies would be better assessed if biotic and abiotic effects could be effectively parsed.

Our overarching aim is to determine how discharge anomalies (floods and droughts of high magnitude and unexpected timing) influence long-term community trajectories of fishes in desert rivers, contrasting responses of the native vs. the non-native assemblage and considering potentially antagonistic biotic interactions between these assemblages. To do this we integrate two time-series methods in a novel way. First, we use the Discrete Fast Fourier Transform (DFFT) to identify the periodic (seasonal) and stochastic (interannual) components of discharge variation, and to extract maximum annual spectral anomalies. Subsequently we combine these discharge anomalies within a multivariate autoregressive state-space (MARSS) modeling framework to quantify and compare the effects of species interactions and discharge anomalies on long-term fish abundances. This framework (Fig. 1) provides a tool for quantifying the relative influences of abiotic and biotic drivers on the native and the non-native assemblages, and especially for disentangling the direct effects of flow, from the flow-mediated effects of non-native fishes, on the native assemblage. In particular, we ask the following chained questions: (i) what are the relative roles of species interactions and discharge anomalies in driving the long-term trajectory (i.e., variation in the relative abundances) of the fish community?; (ii) does the magnitude and direction of these influences differ between the native and the non-native assemblage?; (iii) are eventual differences in responses to discharge anomalies between the native and the non-native assemblage explained by differences in their biological traits?; and finally, (iv) do discharge anomalies influence the spatial patterns of the fish meta-community, measured as beta diversity components across sites?

To answer these questions, we analyzed long-term data on fish abundances from seven sites of the Verde River in Arizona, USA. This river has a flashy hydrograph and a relatively low diversity, with nearly equal

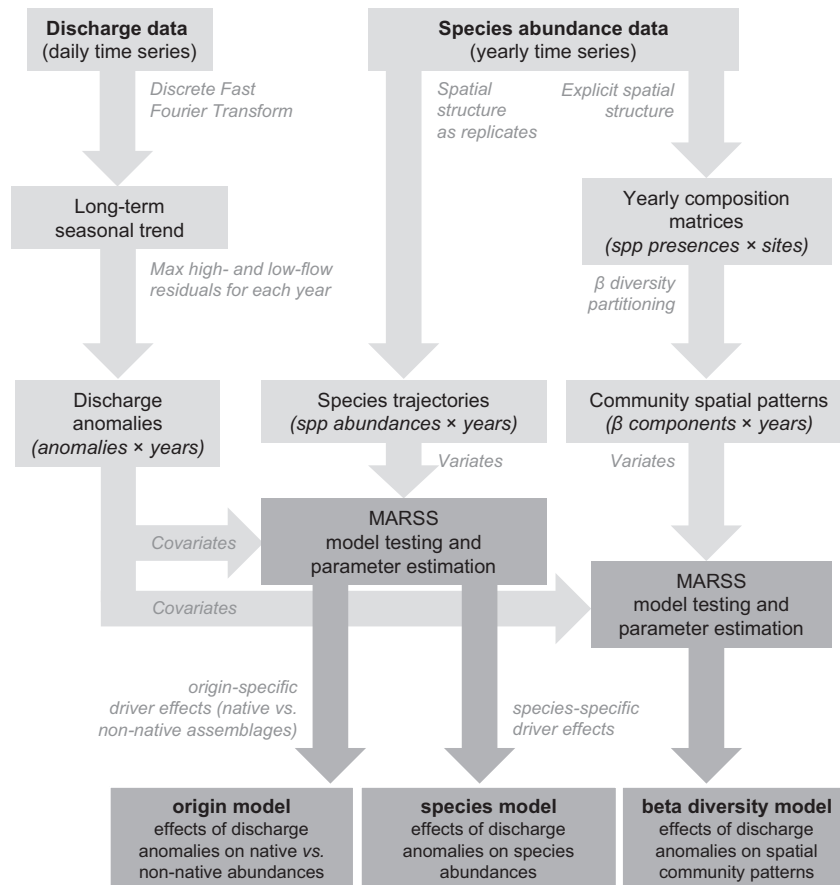


Fig. 1 Flow diagram illustrating the main analyses, from input data (discharge and species abundance time series) to MARSS models outputs (*origin*, *species*, and *beta diversity* models).

numbers of native and non-native species. We predicted that discharge anomalies would be the ultimate driver of long-term trajectories of fish communities in this river, and consequently, that biotic interactions would play only a proximate role (question i). We further predicted that responses would differ between the native and the non-native assemblage (question ii), with biological traits causing native fishes to be impaired by anomalous droughts (but favored by anomalous floods), and non-natives to be benefitted from muted discharge variation (question iii). Finally, we predicted that environmental variation would also influence the (spatial) beta diversity patterns of the fish meta-community, with discharge anomalies determining the relative importance of the two components that contribute to composition dissimilarity across local communities, namely nestedness and turnover (question iv). If these predictions hold true, they would indicate that environmental variation can predict community dynamics even in flashy environments, shedding light on the direction and extent to which anomalous floods and droughts are likely to affect

long-term trajectories of native riverine fauna in the light of global change.

Materials and methods

Study area

We studied the upper Verde River, a major tributary of the Salt River (Gila River basin) in the US state of Arizona. The Verde River flows around 270 km from its headwaters in Big Chino Wash (Prescott National Forest) to its confluence with the Salt River near Phoenix. In 1994, the Rocky Mountain Research Station (USDA Forest Service) established seven monitoring sites from Sullivan Lake to Sycamore Creek (Rinne & Miller, 2006), which were sampled continuously (every April) until 2008. This upper part of the Verde River is relatively undisturbed, without any flow-altering dams or major diversions, and has been an ideal setting to study the abiotic and biotic factors that influence fish assemblage structure in desert rivers (Stefferdud & Rinne, 1995). Sample sites ranged from 150 to 300 m in length and included a variety of aquatic habitats. Backpack electrofishing units were used to sample under debris, banks, and in riffles. For high- and low-gradient

riffles and for glide-runs, shocking was conducted from upstream to downstream, and fish were collected into a 6-m, 3-mm mesh bag seine. Trammel nets (30 m in length and meshes of 13-, 40-, and 80-mm mesh arrays) were employed to sample in deep pools (>2 m). All fishes were counted and returned alive to the stream, and counts from different sampling methodologies were combined at each site and visit. Throughout the 105 recorded samples (7 stations \times 15 years), a total of 16 fish species were detected, of which 6 were native and 10 were non-native. For the present work we dropped from the analyses 2 species with <2% occurrence (both non-native: fathead minnow *Pimephales promelas*, 1.9% occurrence; and largemouth bass *Micropterus salmoides*, 1.0% occurrence). This delivered a final matrix of 14 fish species (6 native, 8 non-native) \times 105 samples. Daily mean discharge data for 45 complete years (from 1/1/1966 to 31/12/2010) were obtained from the US Geological Service (USGS) station 09504000 (Verde River near Clarkdale, AZ, USA).

Stochasticity in discharge variation

We used the Discrete Fast Fourier Transform (DFFT) to identify the characteristic signal of discharge variation in the Verde River, and the residuals or 'anomalies' from this long-term seasonal signal. We then used the maximum (high-flow) or minimum (low-flow) annual anomalies to construct hydrologic (abiotic) variables that would be considered as covariates in the multivariate time-series modeling. Hydrologic variation has been traditionally quantified using recurrence intervals (e.g., with Log-Pearson III distributions). However, such techniques focus on the magnitude of either high- or low-extremes (not both together) and ignore the seasonal occurrence (i.e., timing) of these events; a crucial aspect for ecological applications as biological impacts of high and low flows depend on seasonal base flows (Bunn & Arthington, 2002). Statistical tools borrowed from signal processing, such as the DFFT, provide a means for decomposing variation in discharge into the periodic (seasonal) and stochastic (interannual) components. This allows analyzing discharge series in a more ecologically meaningful way, as extreme forms of stochastic variation (but not predictable, periodic signals) cause ecological disturbance (Lande *et al.*, 2003; Grossman & Sabo, 2010). A complete description of the method employed here is provided in Sabo & Post (2008). Briefly, the DFFT is applied to the time series and the characteristic signals (frequencies, phases, and amplitudes) of seasonal hydrologic variation (i.e., the long-term seasonal trend) are extracted from the power spectrum in the frequency domain. Observed daily events can then be compared to long-term seasonal trend, and residual events (observed - expected discharge) or discharge anomalies can be computed. Anomalies either higher (floods) or lower (droughts) than two standard deviations of the distribution of residual variation around the long-term seasonal can be regarded as *catastrophic events* (Sabo & Post, 2008). Because these events 'carry' information on their magnitude and timing (i.e., they are always of high magnitude and happen 'unexpectedly'), their occurrence may be regarded as a proxy for ecological disturbance (Sabo & Post, 2008; Grossman &

Sabo, 2010). In this study, we computed the long-term seasonal trend for the 45-year discharge series, and identified and extracted the highest- and lowest *annual* discharge anomaly for each year in the time series. This process yielded a new time series of annual maxima (or minima), which could then be used to index each year in terms of high- or low-flow variation for 1993–2007 (hereafter, *discharge anomalies*). We used these discharge anomalies as covariates in the subsequent multivariate time-series models of the fish community (Fig. 1).

Exploring long-term trajectories of fishes using multivariate time-series modeling

We assessed the effects of discharge anomalies and biotic interactions on the trajectories of fish using state-space versions of multivariate autoregressive models. Multivariate autoregressive (MAR) models have been used extensively in econometrics, and in ecology they have been mainly employed to quantify the effects of environmental drivers on species' population growth rates and community dynamics (reviewed in Hampton *et al.*, 2013). Multivariate autoregressive models rely on theory about the patterns of temporal correlation that emerge from environmental drivers and species interactions (Ives *et al.*, 2003). Hence, instead of treating temporal correlation as a nuisance, MAR models use it to estimate effects of drivers vs. interactions on community dynamics. Despite being data-hungry, MAR models are less challenging than mechanistic models, as the latter (but not MAR) require ecophysiological parameters. Moreover, state-space versions of MAR models (i.e., MARSS models) allow inclusion of observation error in the data, which is advantageous because ignoring observation error can fundamentally change our inference about the underlying process (e.g., Knappe & de Valpine, 2012). Our fish count data certainly contained observation error that could potentially bias the measured influence of abiotic and biotic drivers on community dynamics. Therefore, MARSS allowed us to separate the variation in the fish count data due to observation error from the variation due to true population fluctuations. This separation is possible because unlike true population fluctuations, observation error does not influence current or future abundances – it only affects our estimation of that abundance. We used the 'MARSS' R-package (Holmes *et al.*, 2014), which provides support for fitting MARSS models with covariates (i.e., discharge anomalies) to multivariate time-series data (i.e., fish community abundances) via maximum likelihood, using an Expectation–Maximization algorithm. In the matrix form, a MARSS model takes the following form [Eqn (1) is the state process and Eqn (2) is the observation process]:

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

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

Data enter the model as \mathbf{y} (with \mathbf{y}_t being fish abundances modeled as a linear function of the 'hidden' or true abundances, \mathbf{x}_t), and as \mathbf{c}_{t-1} (the lagged covariates, in our case discharge anomalies). In the state process [Eqn (1)], \mathbf{B} is an interaction matrix and models the effect of species on each

other, \mathbf{C} is the matrix whose elements describe the effect of each covariate on each species (hereafter discharge anomaly effects), and \mathbf{w} is a matrix of the process error, with process errors at time t being multivariate normal with mean 0 and covariance matrix \mathbf{Q} . In the observation process [Eqn (2)], \mathbf{v} is a vector of non-process errors, with observation errors at time t being multivariate normal with mean 0 and covariance matrix \mathbf{R} .

We compared two different configurations of the \mathbf{C} matrix. First, we allowed discharge anomaly effects to differ only between native- and non-native species (origin model in Fig. 1). This model was structured to have only four different values in the elements of the \mathbf{C} matrix and hence allowed us to quantify how fishes of native and non-native origin differed (systematically) in their responses to discharge anomalies. Subsequently, we constructed a more complex MARSS model that allowed for species-specific discharge anomaly effects (species model in Fig. 1), thus obtaining as many discharge anomaly effects as the number of species \times discharge anomalies. For both the origin and the species models, we compared several model structures, combining in each case two different configurations of the \mathbf{B} matrix with two different configurations of the \mathbf{R} matrix. In the \mathbf{B} matrix [Eqn (1)], we compared models allowing for biotic interactions (i.e., with all diagonal and off-diagonal coefficients being estimated) with models not allowing for them (using an identity \mathbf{B} matrix, i.e., a diagonal matrix with 1's on the diagonal and 0's elsewhere). In the \mathbf{R} matrix [Eqn (2)], we compared models considering species-specific observation errors with models considering constant observation errors (i.e., equal across all species). For all models we used log-transformed abundances of the 14 fish species as variates, and the discharge anomalies as covariates. Discharge anomaly effects and biotic interaction strengths were assessed via 95% confidence intervals (1000 bootstrap samples).

Biological trait analyses

In addition to MARSS, we also explored whether differences in responses to discharge anomalies between the native and the non-native assemblage could be explained by differences in their biological traits. To this end, we described each fish species in terms of 38 traits using Fish Traits, a database of ecological and life-history traits of freshwater fishes of the United States (Frimpong & Angermeier, 2009). These traits describe the trophic ecology, body size, reproductive ecology, life history, and salinity and habitat preference of the present species (see Table S1 for more details). Replicating the recent approach by Buisson *et al.* (2013), we constructed a multidimensional functional space using Gower's distance for each species pair and a Principal Coordinate Analysis (PCoA). The orthogonal axes provided by the PCoA may be regarded as 'synthetic functional traits summarizing a fish functional niche' (Buisson *et al.*, 2013). Then, the fish species coordinates in the space defined by the PCoA may be used to calculate functional indices. We aimed at obtaining the functional originality and the functional uniqueness of each species. Functional originality was defined as the Euclidean distance to the average position of the species pool (i.e., the centroid of the

fish species coordinates in the space defined by the PCoA), with relatively higher distances to the centroid implying more functionally original fishes. Functional uniqueness was defined as the distance to the nearest neighbor in the functional space, with species falling relatively closer in the functional space being considered more redundant than those being isolated, and hence functionally unique (Buisson *et al.*, 2013). For both functional originality and uniqueness, raw values were standardized by dividing them by the respective maximum value observed among the 14 species. Differences in functional originality and uniqueness between native and non-native fishes were tested using a GLM (1 fixed effect: *origin*). Finally, biological traits typifying the native *vs.* the non-native assemblage were identified by means of a similarity percentages (SIMPER) test (999 permutations, single layout: origin factor). Traits contributing highly and consistently to dissimilarity (i.e., those with dissimilarity/standard deviation >1) were considered to discriminate fish origins (native *vs.* the non-native species). Functional analyses were conducted with Primer v.6 software (Primer-E Ltd, UK) and the 'vegan' R-package (Oksanen *et al.*, 2014).

Spatial patterns of the meta-community

Finally, the spatial extent of our fish data allowed us to examine temporal variation in spatial patterns of diversity. We used a beta diversity partitioning procedure to examine variation in the spatial patterns of the fish meta-community (i.e., the set of the seven studied local communities or monitoring sites). The 'betapart' R-package (Baselga & Orme, 2012) allowed us to quantify overall beta diversity (β_{SOR}) for each year, as well as the relative importance of the two additive components that contribute to β_{SOR} : nestedness (β_{NES}), which indicates 'ordered' species loss and gain, and turnover (β_{SIM}), which indicates species replacements (Baselga, 2010; Baselga & Orme, 2012). We carried out 15 analyses, one for each sampled year (1994–2008), on presence-absence matrices (14 fish species \times 7 sites). Subsequently, we aimed at addressing how β_{SOR} , β_{NES} and β_{SIM} (variates) responded to discharge anomalies (covariates) with an additional MARSS model (Fig. 1), but one in which the variates were a matrix of beta diversity components rather than species abundances. We considered component-specific observation error and all possible interactions of discharge covariates on the beta diversity components (β_{SOR} , β_{NES} , and β_{SIM}). As with our analysis of the temporal dynamics of the global community, we were again interested in quantifying the discharge anomaly effects. We assessed these effects via 95% confidence intervals (obtained numerically after 1000 bootstrap samples). We refer to this model hereafter as *beta diversity model* (Fig. 1).

Results

Discharge anomalies overview

The long-term seasonal trend extracted with the DFFT (red line in Fig. 2a) showed low basal flows and a

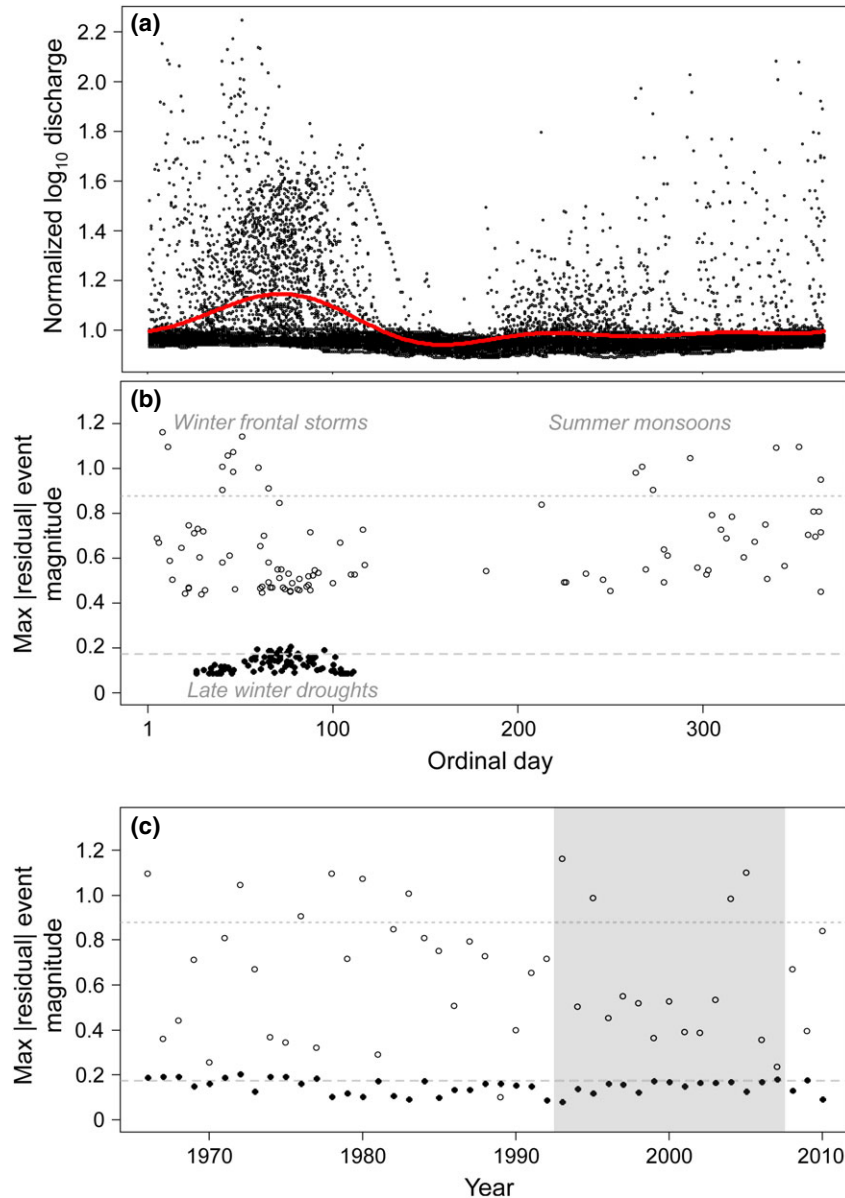


Fig. 2 Summary of 45 years (1966–2010) of daily mean discharge data in the upper Verde River. (a) Hydrograph showing daily average discharge (black dots) in normalized \log_{10} -transformed units (originally measured as cfps, from USGS data). The long-term seasonal trend extracted from DFFT is shown as solid red. (b) Timing of the high flow anomalies (empty circles) and the low-flow anomalies (black circles) recorded for the whole discharge series ($|\text{residuals}|$ for comparison). Discontinuous lines show the threshold corresponding to 2 standard deviations of the distribution of all residual flows across the 45-year record (dotted line for high flows; dashed line for low flows). Empty circles above the dotted line, and black circles above the dashed line, indicate catastrophic floods and droughts, respectively. For 'ordinal day', day 1 is January 1st. The approximate timing of winter frontal storms and summer monsoons, and of late winter droughts, is shown. (c) Magnitude of maximum residual high flow events (empty circles) and low-flow events (black circles) across the 45-year record ($|\text{residuals}|$ for comparison). Discontinuous lines show the threshold corresponding to 2 standard deviations of the distribution of all residual flows across the 45-y record, for high flows (dotted line) and for low flows (dashed line). Empty circles above the dotted line, and black circles above the dashed line, indicate catastrophic floods and droughts, respectively. The gray-shaded area shows the 15-year period (1993–2007) that was coupled with fish data.

seasonal peak in late winter. High flow anomalies generally occurred in two distinct periods (summer monsoons and winter frontal storms), whereas low-flow

anomalies were clustered around later winter, between mid-January to mid-April (Fig. 2b). A long drought (9 years, 1984–1992) immediately preceded our 15-year

study (shaded area in Fig. 2c; years 1993–2007). Our 15-year period encompassed both wet (1993–1995, 2004–2005) and dry periods (1996–2003, 2006–2007), and started with the most extreme high flow event observed across the entire series (in 1993). Overall, this 15-year period encompassed a total of four catastrophic high flow events and nine low-flow events that were either immediately below or above the catastrophic threshold.

Discharge anomaly effects on the long-term trajectories of fishes

The native and the non-native assemblages demonstrated large fluctuations in abundance and a general negative co-variation (Figure S1). The best (lowest AICc) origin model (the model where the effect of environmental drivers is determined by whether the species is native or non-native; Fig. 1) was the one considering species-specific observation errors and origin-specific biotic interactions (i.e., allowing effects of non-native on native species and *vice versa*, as well as effects within the native and within the non-native assemblage; model 1 in Table 1). The support for this model was higher than that observed for the best *species model* (the effect of environmental drivers is determined by species regardless of whether it is native or non-native; Fig. 1), implying that fish responses to discharge anomalies could be safely summarized as native vs. non-native responses. For the species models, species-specific observation errors were also better supported, but the model not allowing species-specific biotic interactions received virtually the same support as the one allowing species-specific biotic interactions (AICc = 1104.2 and 1104.6, respectively; models 5 and 6 in Table 1). To assess if selecting one of these species models would change our inference about the drivers,

we compared the discharge anomaly effects estimated by this pair of models (Figure S2). Both models 5 and 6 provided a similar inference about the drivers (Figure S2). Therefore, for the sake of simplicity we selected model 6 as the best species model.

After bootstrapping the discharge anomaly effects estimated by the origin model (model 1), we observed that native fishes responded positively to high-, and negatively to low-flow anomalies (Fig. 3a). In contrast, anomalies did not significantly influence long-term abundances of non-native fishes (Fig. 3a). Biotic interaction strengths between the native and the non-native assemblages were significant in both directions (Fig. 3b), but much closer to zero than the discharge anomaly effects. By bootstrapping the discharge anomaly effects of the species model (model 6) we were able to identify which were the species most and least affected by discharge anomalies. Three native species responded significantly and positively to high flow anomalies (the desert sucker *Catostomus clarki*, the sonora sucker *Catostomus insignis*, and the roundtail chub *Gila robusta*), with this same set fishes responding negatively to low-flow anomalies (Fig. 4). As observed in the origin model, most of the non-native species of the species model appeared to be less responsive. The only exception was the green sunfish *Lepomis cyanellus*, which was significantly favored by droughts (Fig. 4).

Biological traits of the native vs. the non-native assemblage

To test if differences in the responses to discharge anomalies between the native and the non-native assemblage (as observed in the species and origin models) could be explained by an adaptive suite of traits, we contrasted assemblages based on their functional

Table 1 Summary of the model selection approach of the MARSS origin (models 1 to 4) and species models (models 5 to 8). For model types, two different structures on the process model (Eqn 1; biotic interactions allowed *vs.* not allowed) were combined with two different structures on the observation model (Eqn 2; species-specific *vs.* constant observation error). All models were run on log-transformed abundances of fish species as variates and discharge anomalies as covariates, and allowed origin-specific (for the origin model) or species-specific (for the species model) effects of the covariates on the variates. The different *origin* and *species models* are ordered from strongest to weakest support (based on AICc), and the AICc of each model is compared to the AICc of the top model (i.e., *origin model* with origin-specific biotic interactions and species-specific observation error)

Model		Biotic interactions	Observation errors	AICc	AICc-min(AICc)
Origin-specific discharge anomaly effects	1	Origin-specific	Species-specific	970.7	0
	2	None	Species-specific	1078.0	107.4
	3	Origin-specific	Constant	1395.7	425.0
	4	None	Constant	1509.7	539.0
Species-specific discharge anomaly effects	5	Species-specific	Species-specific	1104.2	133.5
	6	None	Species-specific	1104.6	133.9
	7	Species-specific	Constant	1559.3	588.6
	8	None	Constant	1538.2	567.5

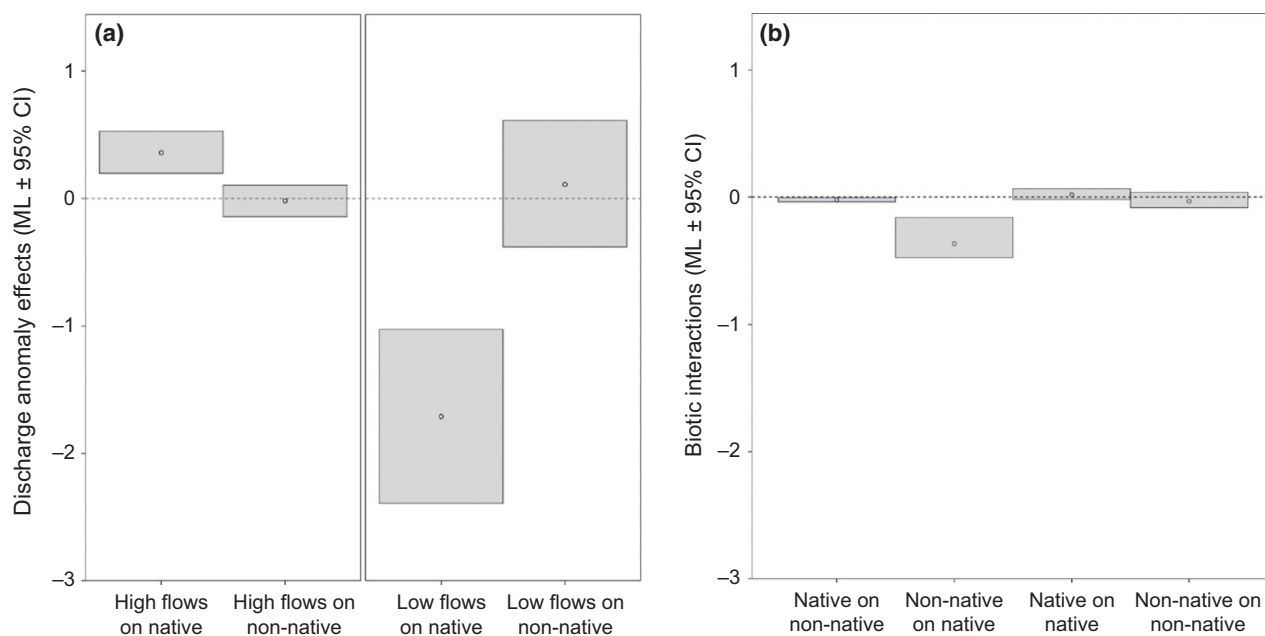


Fig. 3 Bootstrapped parameters of the best MARSS origin model (model 1 in Table 1). (a) Discharge anomaly effects on native *vs.* non-native species. (b) Biotic interactions (i.e., interaction strengths) between the native and the non-native assemblages, and within the native and the non-native assemblages. The maximum likelihood (ML) of each parameter and the corresponding 95% confidence intervals (CI) were obtained after 1000 bootstrap samples.

originality and uniqueness, and on their typifying traits. Functional originality did not differ between native and non-native fishes (GLM; $F_{1,12} = 2.232$, $P = 0.161$; Table 2), but functional uniqueness was significantly higher in native species (GLM; $F_{1,12} = 4.951$, $P = 0.046$; Table 2). When investigating individual traits we identified 9 strategies (describing body size, habitat preference, life history and trophic ecology of the fishes) that typified native relative to non-native species (Table 3).

Discharge anomaly effects on the spatial patterns of the meta-community

Beta diversity partitioning showed that the turnover component (β_{SIM}) dominated over the nestedness component (β_{NES}) in explaining overall beta diversity (β_{SOR}) (mean \pm SD: β_{SOR} , 0.438 ± 0.092 ; β_{SIM} , 0.248 ± 0.129 ; β_{NES} , 0.190 ± 0.094). More importantly, the relative importance of these components was not constant across the 15-year period: despite turnover generally dominating, in some years spatial dissimilarity was largely or totally explained by the nestedness component (Figure S3). The MARSS beta diversity model showed that discharge anomalies played a significant role in explaining transitions between beta diversity patterns dominated by nestedness *vs.* turnover, with high flow anomalies diminishing, and low-flow anomalies increasing, the relative contribution of nestedness

(Fig. 5). This result implies that after anomalous droughts (but not after anomalous floods), beta diversity was largely explained by variation in species richness among local communities.

Discussion

Quantifying the relative roles of environmental variation and species interactions in determining the resilience of ecological communities to various components of global change is challenging but essential to better understand biological responses to increased climate variability (Staudt *et al.*, 2013; Thornton *et al.*, 2014). In this study, we present a powerful and transferable approach to quantifying joint effects of climate and other stressors on the resilience of biological communities. We used this approach to show how anomalous floods and droughts can influence long-term trajectories of native fish in highly variable rivers that have been invaded by non-native faunas. This topic has been the focus of a considerable amount of research in both riverine (e.g., Seegrist & Gard, 1972; Bernardo *et al.*, 2003; Propst *et al.*, 2008; Gido & Propst, 2012) and riparian ecosystems (e.g., Sher *et al.*, 2002; Nagler *et al.*, 2005; Stromberg *et al.*, 2007a,b; Catford *et al.*, 2011; Vivian *et al.*, 2014). Generally, the riverine studies suggest that hydrology is an important driver of abundance of both natives and non-natives (Seegrist & Gard, 1972; Bernardo *et al.*, 2003; Propst *et al.*, 2008) and that

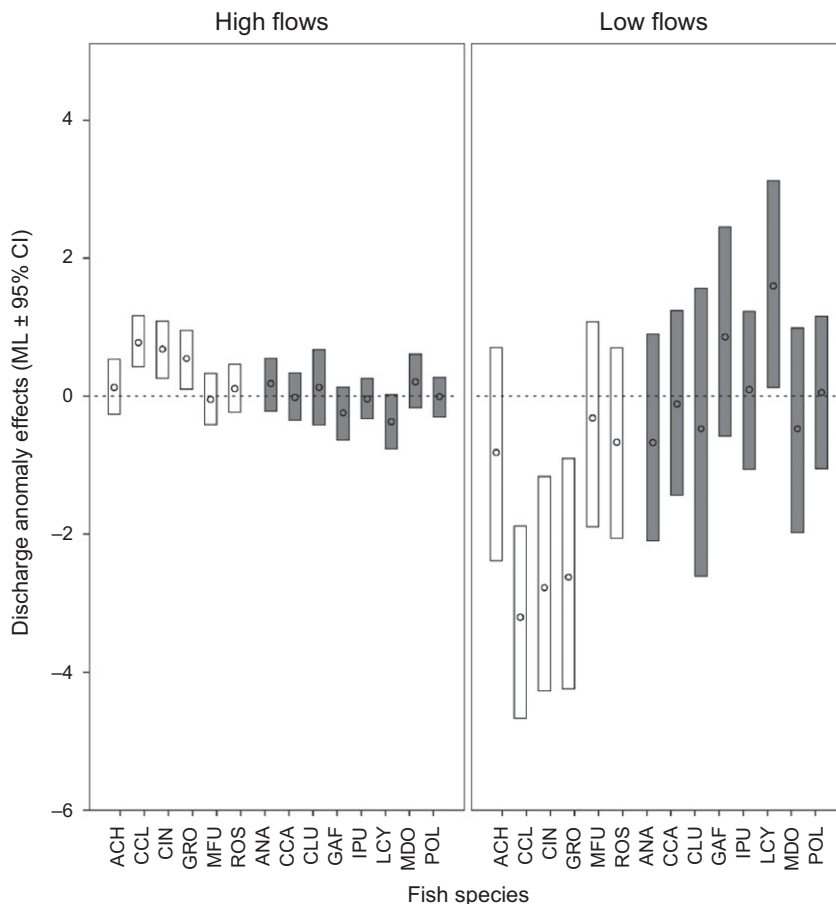


Fig. 4 Bootstrapped parameters of the best MARSS species model (model 6 in Table 1). The discharge anomaly effects for each fish species are shown (white bars = native species, grey bars = non-native species). The maximum likelihood (ML) of each C parameter and the corresponding 95% confidence intervals (CI) were obtained after 1000 bootstrap samples. Native fishes: ACH = Longfin dace, CCL = Desert sucker, CIN = Sonora sucker, GRO = Roundtail chub, MFU = Spike dace, ROS = Speckled dace. Non-native fishes: ANA = Yellow bullhead, CCA = Common carp, CLU = Red shiner, GAF = Mosquitofish, IPU = Channel catfish, LCY = Green sunfish, MDO = Smallmouth bass, POL = Flathead catfish.

non-native species outcompete or over exploit native species (Propst *et al.*, 2008; Gido & Propst, 2012). In contrast, most riparian studies have found that hydrology supersedes species interactions – flow alterations preclude native species and promote the dominance non-native species, with little effect of non-natives on natives (Nagler *et al.*, 2005; Stromberg *et al.*, 2007a,b). Within this context, recent work has suggested that successful management of native riparian plant communities may be achieved by mimicking –if water allocations permit – natural disturbance regimes (Catford *et al.*, 2011; Vivian *et al.*, 2014). Consistent with this riparian work, we found support for the notion that discharge variation was paramount and superseded species interactions in determining community composition at multiple scales. In our system, native species responded negatively to low-flow anomalies but were resilient to high-flow anomalies; non-native species by

contrast exhibited no significant response and the effect of non-native species on native fishes was secondary to the direct effects of drought. Biological traits typified a functionally unique native assemblage and explained the observation that droughts negatively impacted, but floods favored, the native assemblage. Furthermore, the abiotic paradigm was evident not only in the fishes' temporal trends but also in the variation in their spatial patterns, with discharge anomalies influencing composition dissimilarity patterns across the meta-community.

Discharge anomalies, not non-native species, determine trajectories of native fish

The notion that seasonal flooding has differential effects on native and non-native freshwater faunas has a long history dating to Seegrist & Gard (1972), who reported

Table 2 Global relative abundance ('Abund', in %), functional originality ('FOri') and functional uniqueness ('FUni') of the fish species considered in the study. Functional originality and uniqueness were obtained after Buisson *et al.* (2013), using traits compiled in the Fish Traits database (Frimpong & Angermeier, 2009) (see complete list and description of traits in Table S1)

	Code	English name	Latin name	Abund	FOri	FUni
Native	ACH	Longfin dace	<i>Agosia chryogaster</i>	5.2	0.782	0.783
	CCL	Desert sucker	<i>Catostomus clarki</i>	20.6	0.667	0.822
	CIN	Sonora sucker	<i>Catostomus insignis</i>	16.5	0.682	1.000
	GRO	Roundtail chub	<i>Gila robusta</i>	5.9	0.583	0.900
	MFU	Spike dace	<i>Meda fulgida</i>	2.0	0.758	0.860
	ROS	Speckled dace	<i>Rhinichthys osculus</i>	0.9	0.834	0.919
Non-native	ANA	Yellow bullhead	<i>Ameiurus natalis</i>	1.2	0.807	0.860
	CCA	Common carp	<i>Cyprinus carpio</i>	0.4	0.694	0.783
	CLU	Red shiner	<i>Cyprinella lutrensis</i>	38.8	1.000	0.825
	GAF	Mosquitofish	<i>Gambusia affinis</i>	2.0	0.985	0.793
	IPU	Channel catfish	<i>Ictalurus punctatus</i>	<0.1	0.721	0.738
	LCY	Green sunfish	<i>Lepomis cyanellus</i>	2.5	0.708	0.840
	MDO	Smallmouth bass	<i>Micropterus dolomieu</i>	3.9	0.666	0.850
	POL	Flathead catfish	<i>Pylodictis olivaris</i>	<0.1	0.951	0.793

Table 3 Similarity percentages (SIMPER) analysis identifying the traits that typify native *vs.* non-native species. The average abundance of each trait is shown for native ('Native') and for non-native ('Non-native') species, and bolded in whichever category is higher. Only traits contributing highly and consistently to dissimilarity between these categories, i.e., those with dissimilarity/standard deviation ('Diss/SD') >1, are shown. Contributions to dissimilarity ('Contrib%') are also shown. Maxtl = maximum total length in cm, lacustrine = preference for lentic systems, modcurr = preference for moderate current, claysilt = preference for clay or silt substrate, season = the sum of the proportions of each month in which spawning occurs, approximating the length of the spawning season, longevity = longevity in years based on life in the wild wherever available, serial = serial or batch spawner, fshcrb = trophic preference for large fishes, crayfishes, crabs, and frogs, detritus = trophic preference for detritus or unidentifiable vegetative matter. We used the traits compiled in the Fish Traits database (Frimpong & Angermeier, 2009) (see complete list and description of traits in Table S1)

Trait type	Trait	Native	Non-native	Diss/SD	Contrib%
Body size	Maxtl	4.12	9.41	1.17	3.02
Habitat	Lacustrine	2.08	10.94	1.62	3.88
preference	Modcurr	11.11	4.17	1.20	2.63
	Claysilt	4.76	8.93	1.02	3.08
Life history	Season	8.15	6.38	1.24	2.00
	Longevity	4.90	8.82	1.10	2.41
	Serial	9.52	5.36	1.01	3.19
Trophic ecology	Fshcrb	2.78	10.42	1.11	4.12
	Detritus	9.52	5.36	1.03	3.18

that the negative covariation between native and introduced trout (Salmonidae) in Sagehen Creek (California, USA) was explained by alterations to the natural flow

regime. There, seasonal winter floods favored native salmonid life histories (spring spawners) but not non-native life histories (fall spawners); whereas minor spring floods destroyed native salmonid eggs, thereby enhancing survival of young non-native salmonids. Since then, several studies have demonstrated different responses of native and non-native fishes to seasonal flows, especially in other arid-land rivers in the American Southwest (Tyus & Saunders, 2000; Eby *et al.*, 2003; Propst *et al.*, 2008; Gido & Propst, 2012; Gido *et al.*, 2013). These studies generally show opposite effects of streamflow features on natives and non-natives, and/or significant antagonistic interactions of the non-native assemblage (or some particular non-native species) on the natives.

Our results enrich the findings of these previous studies in at least two ways. First, our DFFT-MARSS framework allowed us to explicitly measure the relative effects of biotic and abiotic drivers of variance in stream fish abundances and we observed only weak biotic effects on the long-term trajectory of the fish community as a whole. Species interactions (captured by the *B* matrix) were non-significant in the species model, and negative but much less important than discharge anomaly effects (in the *C* matrix) when considering the global effects of the non-native on the native assemblage in the origin model. Second, the effects of discharge variation on native and non-native fishes were different but surprisingly not opposite in sign. In contrast to strong negative effects of low-flow anomalies on native species, the non-native assemblage was largely unresponsive to high- or low-flow variation (as measured by anomalies). Hence, abundances of native species varied due to significant environmental variation (high- and

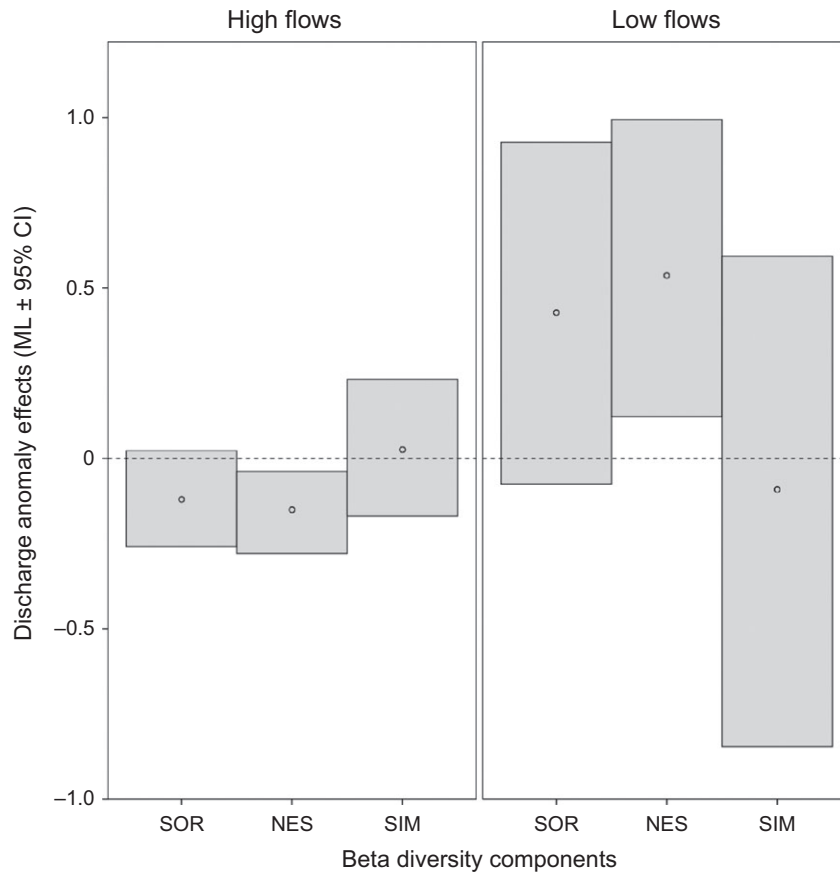


Fig. 5 Bootstrapped parameters of the MARSS beta diversity model. The discharge anomaly effects on overall beta diversity (β_{SOR}) and its components (nestedness, β_{NES} ; turnover, β_{SIM}) are shown. The maximum likelihood (ML) of each C parameter and the corresponding 95% confidence intervals (CI) were obtained after 1000 bootstrap samples.

low-flows) and in spite of a relatively more constant baseline of non-natives.

The context of our results is also important and differs from previous work that has drawn different conclusions. First, our system experiences large flow variation. Disturbance is known to alter competitive interactions among species (Byers, 2002). Therefore, species interactions may indeed be relevant in more stable rivers, such as desert rivers with managed flows (Gido & Propst, 2012; Gido *et al.*, 2013) or rivers under hydroclimates with lower catastrophic variation (i.e., Mediterranean rather than arid and semiarid Koppen climate types; Seegrist & Gard, 1972; Bernardo *et al.*, 2003). Second, the effects of non-native species on native species' persistence may strongly depend on the identity of the non-native species (Bunn & Arthington, 2002; Pusey *et al.*, 2006). Gido & Propst (2012) found that the channel catfish *Ictalurus punctatus* was included in the top-ranked models predicting native abundances in the San Juan River (New Mexico and Utah, USA), but in our study, this predator was extremely scarce, as

also was the flathead catfish *Pylodictis olivaris* (both represented <0.1% of the global abundance; Table 2). Although small-bodied non-native fishes like the red shiner *Cyprinella lutrensis* (by far the most abundant species in our study) have been found to prey on larvae of native fishes (Ruppert *et al.*, 1993; Brandenburg & Gido, 1999), these interactions did not influence our native assemblage. Overall, our results suggest that even when biotic interactions are potentially relevant, faunal communities in highly variable environments may be driven predominantly by environmental variation (abiotic paradigm).

Droughts decimate the native assemblage and lead to 'functional debt'

The term *lentification* has been recently coined to describe the widely observed transformation of rivers from lotic to lentic habitats (Sabater, 2008). The fact that native species are severely affected by anomalous droughts in our system is very relevant when consider-

ing the impacts of lenticification on biodiversity. In the Southwest United States, the equivalent of nearly 76% of streamflow is being currently appropriated by humans, and this figure could increase if demographic projections that predict a doubling of the super-region's population within this century come true (Sabo *et al.*, 2010a). More importantly, in the American Southwest high human water appropriation is interacting with a transition to a more arid climate (Seager *et al.*, 2007; Karl *et al.*, 2009). Our study suggests that if frequency and magnitude of droughts increase in southwestern rivers and anomalous droughts (due to high intensity or aseasonal timing) become the new normal, functionally homogenized fish communities with low prevalence of native members are to be expected.

We found that the native, but unexpectedly not the non-native assemblage, responded to discharge anomalies. The general lack of response of non-natives apparently contradicts previous studies suggesting that natural flow regimes should provide environmental resistance to the spread of non-native species (Kiernan *et al.*, 2012; Gido *et al.*, 2013; Mims & Olden, 2013). Those views are based on the 'natural flow regime' concept (Poff *et al.*, 1997), which implies that non-native organisms that evolved in systems with different suites of abiotic features should not find suitable conditions in systems with natural regimes (Lytle & Poff, 2004). In our study, only the green sunfish *Lepomis cyanellus* benefitted from the anomalous droughts that were negatively associated with native abundances, and no non-natives were reduced in abundance by the floods that were positively associated with native abundance. Whereas the positive response of green sunfish to anomalous droughts is in agreement with its high preference for slow current conditions and lacustrine habitats (Frimpong & Angermeier, 2009; Gibson *et al.*, 2014; Pool & Olden, 2014), non-natives not responding to anomalous floods is a more intriguing outcome. We offer two explanations for the observed lack of response by non-natives: (i) catastrophic floods (4 events during the studied period and 6 preceding it) were perhaps not intense enough to influence the non-native assemblage; or (ii) non-natives indeed responded (negatively) to flow variation on the short-term but recolonized quickly, so that analyses of long-term trajectories would not reflect such responses. Historical flow data suggest that the first hypothesis is highly unlikely, since our fish time series started with the most extreme floods recorded throughout the whole 45-year period (including a 100-year recurrence event), which dramatically altered stream channel morphology and the aquatic habitats of the upper Verde River (Rinne & Stefferud, 1998). In contrast, the second hypothesis seems plausible as other studies have

reported that non-native fishes in arid-land rivers are highly resilient. Pool & Olden (2014) found that an experimental flood from Alamo Dam (Bill Williams River basin, western Arizona) elicited a short-term reduction in the abundance of non-native species in sites downstream to the dam, but the pre-flood composition (similar to that of the upper Verde River) was recovered shortly after the event. Given the temporal resolution we employed (yearly spaced, with a variable lag of several months between the high flow event and the spring fish sampling), it is likely that we missed such short-term responses. This suggests that flow management may be able to enhance the native components of the assemblage and boost the ratio of native: non-native abundance, but mechanical removal may need to be invoked to manage the non-native assemblage in the long term.

As expected, biological traits offered a mechanistic explanation for the effects of hydrology on the relative persistence of native and non-native fishes. Traits conferring resilience from or resistance against flood disturbance typified the native assemblage. These traits included: habitat preference for moderate current and not for lacustrine systems, long spawning seasons and short longevities, or trophic preference for detritus and not for large macroinvertebrates and other vertebrates. Similarly, a study that paired flow-regulated and free-flowing rivers across the United States found that fish assemblages in free-flowing locations, relative to assemblages below dams, were characterized by a relatively lower proportion of equilibrium species (species with strategies favored in more stable, predictable environments) (Mims & Olden, 2013). Our analyses show that trait combinations of the native component were also more unique (*sensu* Buisson *et al.*, 2013). This result contributes to the notion that generally extirpations do not occur randomly, but elicit disproportionate functional homogenization (Pool & Olden, 2012). Of the three drought-sensitive native species of our study, the Sonora sucker *Catostomus insignis* and the Roundtail chub *Gila robusta* fall under the *threatened* IUCN category, with the latter additionally being a candidate endangered species under the Endangered Species Act criteria. We observed both species were, at the same time, very functionally unique (≥ 0.9 of a possible 1, Table 2). Functional homogenization had previously been attributed to the contributions of non-native species on the assemblage as a whole (Rahel, 2002; Pool & Olden, 2012). Here, we demonstrate that anomalous droughts may induce a 'functional debt' whereby trait combinations disappearing as a consequence of the extirpation of drought-sensitive native species will probably not be offset by the trait combinations of the remaining drought-resistant non-natives.

Environmental variation drives meta-community diversity patterns

Investigating beta diversity patterns is key to understanding meta-community dynamics and the relative importance of deterministic vs. stochastic processes (Chase & Myers, 2011). Beta diversity partitioning has lately become a popular tool in community ecology because it allows disentangling the relative contributions of variation in species richness and in species identities to overall composition dissimilarity (Baselga, 2010; Baselga & Orme, 2012; Legendre, 2014). Although beta diversity (β_{SOR}) and its additive components (nestedness β_{NES} , and turnover β_{SIM}) are usually studied across space (e.g., Gossner *et al.*, 2013; Nascimbene *et al.*, 2013; Escoriza & Ruhí, 2014), some studies have examined them through time to assess global change impacts on the spatial patterns of biodiversity (Albouy *et al.*, 2012; Angeler, 2013). To our knowledge our study is the first to integrate environmental covariates (here discharge anomalies) with beta diversity and its components (as variates) in the context of stochastic modeling of time series (beta diversity model). This analysis revealed that different types of hydrological extremes lead to different meta-community patterns, with anomalous droughts increasing, and anomalous floods decreasing, the relative importance of nestedness (β_{NES}).

Nestedness is widespread in freshwater biotas (Heino, 2011; Batzer & Ruhí, 2013; Tornés & Ruhí, 2013) and habitat suitability is known to influence this structure (Heino & Muotka, 2005; McAbendroth *et al.*, 2005). Therefore, results from the *beta diversity model* were not only expected but also congruent with the origin and species models, as low flows differentially harming the native assemblage should 'naturally' generate a nested meta-community (see schematization in Fig. 6). In this way, the unresponsive non-native assemblage constituted a core set of taxa present in virtually every local community, whereas some drought-sensitive species disappeared from the most physically adverse sites after anomalous droughts. Differential extinction and selective environmental tolerances are well-known determinants of nestedness (Ulrich *et al.*, 2009). Our study exemplifies these mechanisms and further shows that successive nestedness- and turnover-dominated scenarios may be explained by low resistance, but high resilience, of part of the assemblage (*sensu* Connell & Sousa, 1983). Overall, seasonal floods are essential to maintain mixed assemblages of native and non-native fishes as only by preserving meta-community dynamics, the drought-sensitive assemblage can bounce back to pre-drought conditions after this disturbance.

Implications of the current findings

In this study we quantified the stochastic component of discharge and integrated this variation directly into community time-series models. Our results suggest that stochastic variation can predict community composition and its spatial variability even in very flashy environments, offering an alternative but effective way to understand how hydroclimatic anomalies and invasive species can affect long-term trajectories of native riverine fauna. Climate and invasion are two key components of global change (Staudt *et al.*, 2013), and well recognized drivers of freshwater fish extinctions (Xenopoulos *et al.*, 2005; Rahel & Olden, 2008). Disentangling their effects on native assemblages is crucial to anticipating the ecological impacts of new hydrological regimes. Although stream and riparian ecosystems in the American Southwest are subject to frequent hydro-

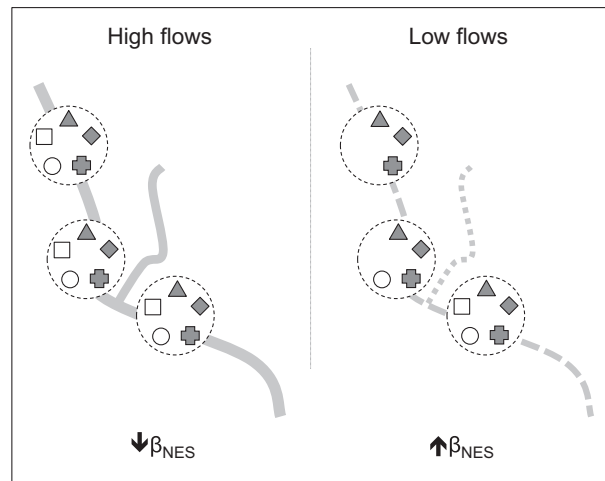


Fig. 6 Illustration of results from the beta diversity model. Overall spatial dissimilarity within a meta-community (i.e., beta diversity, β_{SOR}) may be explained by a combination of two components, namely nestedness or species gain and loss (β_{NES}), and turnover or species replacements (β_{SIM}). In the schematization, local communities are represented by dashed circles and species are represented by small shapes within the dashed circles (empty shapes are native species; full shapes non-native ones). The *origin* and *species models* showed that some (but not all) members of the regional pool of species were sensitive to hydrologic extremes, with the sensitive subset responding oppositely to high and low flows. Thus, the non-sensitive subset (i.e., non-native species) could be potentially present in all local communities regardless of the hydrological context, whereas the sensitive subset (i.e., native species) could be locally extirpated under the harmful hydrological extreme. These differential responses should elicit a nested structure under low- but not under high flow anomalies, which is congruent with the discharge anomaly effects described by the beta diversity model (Fig. 5).

logical disturbance (Grimm *et al.*, 1997; Sponseller *et al.*, 2010), our results suggest that anomalous droughts (in timing and/or magnitude) are impairing fish communities both taxonomically and functionally. As drought severity increases with projected climate change and groundwater depletion, native biodiversity losses are to be expected in desert rivers of the American Southwest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Long-term trajectories (1994–2008) of total native and non-native fish abundance across the seven monitoring sites and globally.

Figure S2. Comparison of the discharge anomaly effects estimated by the two *species models* that received highest support [model 5, AICc = 1104.2; model 6, AICc = 1104.6; see Table 1].

Figure S3. Results of the Beta diversity partitioning. The relative contributions of the nestedness (β_{NES}) and the turnover (β_{SIM}) components to overall beta diversity (β_{SOR}) across the studied period 1994–2008 are shown.

Table S1. List, data scale and description of the biological traits considered in this study.