ECOLOGY OF FRESHWATER FISH

Multiple watershed alterations influence fish community structure in Great Plains prairie streams

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Abstract – Stream fish distributions are commonly linked to environmental disturbances affecting terrestrial landscapes. In Great Plains prairie streams, the independent and interactive effects of watershed impoundments and land cover changes remain poorly understood despite their prevalence and assumed contribution to declining stream fish diversity. We used structural equation models and fish community samples from third-order streams in the Kansas River and Arkansas River basins of Kansas, USA to test the simultaneous effects of geographic location, terrestrial landscape alteration, watershed impoundments and local habitat on species richness for stream-associated and impoundment-associated habitat guilds. Watershed impoundment density increased from west to east in both basins, while per cent altered terrestrial landscape (urbanisation + row-crop agriculture) averaged ~50% in the west, declined throughout the Flint Hills ecoregion and increased (Kansas River basin ~80%) or decreased (Arkansas River basin ~30%) to the east. Geographic location had the strongest effect on richness for both guilds across basins, supporting known zoogeography patterns. In addition to location, impoundment species richness was positively correlated with local habitat in both basins; whereas stream-species richness was negatively correlated with landscape alterations (Kansas River basin) or landscape alterations and watershed impoundments (Arkansas River basin). These findings suggest that convergences in the relative proportions of impoundment and stream species (i.e., community structure) in the eastern extent of both basins are related to positive effects of increased habitat opportunities for impoundment species and negative effects caused by landscape alterations (Kansas River basin) or landscape alterations plus watershed impoundments (Arkansas River basin) for stream species.

Key words: watershed; impoundments; fish community; Great Plains; streams

Introduction

Lotic freshwater ecosystems are strongly influenced by terrestrial land use alterations involving human extraction and exploitation of ecosystem goods and services (Likens et al. 1978; Richards et al. 1996). Agricultural land cover in particular contributes to reduced habitat suitability and degraded integrity of fish communities in surrounding streams (Wang et al. 1997). Such strong linkages between terrestrial landscape alterations and stream biota are mediated by cascading mechanisms involving hydrologic connectivity, or the movement of matter, energy and organisms through stream corridors (Pringle 2001). The mechanisms that maintain hydrologic connectivity include hydrology, geomorphology, erosion and deposition, such as run-off, channel shape, sediment movement and substrate composition respectively. These elements collectivity represents the land cover cascade (LCC), a framework used to quantify the transfer of land-cover-disturbance effects to stream biota such as fishes or aquatic invertebrates (Burcher et al. 2007). These landscape alterations have been implicated in the altered distributions of aquatic biota

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across a range of spatiotemporal scales (Cooper et al. 2013; Bouska & Whitledge 2014). However, assigning cause to individual landscape alterations is challenging for a number of reasons, including covariation among natural and anthropogenic gradients, multiple mechanisms of change operating simultaneously and in nonlinear fashions, and uncertainty in separating historical and contemporary influences (Allan 2004). New statistical frameworks such as structural equation modelling (SEM) directly address these limitations and are increasingly applied to assess relationships between multiple forms of landscape change and stream ecosystem health (Maloney & Weller 2011; Bizzi et al. 2013).

Impoundment construction is a unique form of landscape change that has drastically altered ecosystems throughout the world, with over 16.7 million occurring globally (Lehner et al. 2011). Large impoundments (>200 ha) inundate vast extents of lotic habitat and transform terrestrial habitat into lentic aquatic habitat. These transformations affect fishes through a variety of pathways, including altering habitat mosaics within a reservoir, manipulating downstream flow regimes and serving as sources of invasion into adjacent aquatic habitats (Havel et al. 2005; Falke & Gido 2006; Johnson et al. 2008). Small impoundments (<200 ha) are more numerous, and similar transformations occur on differing scales. At local scales, small impoundments inundate small areas of the landscape; however, summing transformations by these impoundments within a stream catchment (watershed hereafter) might have detectable effects at spatial scales comparable to large reservoirs, especially in the context of hydrologic connectivity (Pringle 2001). For example, watershed impoundments retain run-off and dampen small flow pulses (Earl & Wood 2002), which consequently change downstream flow regimes and channel morphologies (DeCoursey 1975; Schoof et al. 1987; Friedman et al. 1998). These processes represent the critical components of the LCC as described by Burcher et al. (2007), except that here the context involves transformation of terrestrial-to-aquatic habitat within a watershed rather than conversion of one terrestrial land cover to another. Although available aquatic habitat within a watershed is positively associated with integrity of warm water fish communities (Wang et al. 1997), effects of watershed impoundments on obligate stream fishes are generally considered negative (Schrank et al. 2001; Mammoliti 2002). Separating natural aquatic habitats such as streams or natural lakes from anthropogenic watershed impoundments might aid in identifying the mechanisms that control total species richness (Wang et al. 1997) versus richness of fishes uniquely adapted to streams (i.e., stream versus impoundment

species diversity; Mammoliti 2002). Given that land cover transitions from native cover to urban and agriculture occur simultaneously with construction of impoundments, additional research is necessary to determine the relative effects of these alterations as well as how these alterations influence fishes with contrasting habitat associations.

Great Plains prairie streams represent ecosystems afflicted by substantial watershed alteration. Contemporary Great Plains watersheds are dominated by row-crop agriculture, urbanisation or cattle-grazing practices (Dodds et al. 2004), and in many regions of the Great Plains, >90% of native land cover has been transformed for human use (Gido et al. 2010). These transformations influence water quality, invertebrate community composition and distribution of stream fishes (Whiles et al. 2000; Gido et al. 2006; Dodds & Oakes 2008). Watershed impoundments are also implicated in the decline of some native species (Schrank et al. 2001; Gerken & Paukert 2013) and concurrent with the expansion of others (Gido et al. 2010). Whereas changes in lotic fish community structure in larger rivers are related to the combined effects of habitat fragmentation and stream dewatering (Perkin et al. 2014), species distributions in smaller streams are more intimately related to landscape alterations in the watersheds (Troia & Gido 2013). In these smaller streams, fish species richness is related to stream size, land cover variables and geological characteristics (Gido et al. 2006), but the effects of habitat alteration and fish invasions caused by watershed impoundments are largely unaddressed despite recognition of the potential for degradation (Dodds et al. 2004). The extent to which widespread construction of watershed impoundments in the Great Plains has contributed to altered fish diversity remains unclear. Furthermore, the relative impacts of watershed impoundments compared to other forms of terrestrial land cover change (e.g., conversion of prairie to row-crop agriculture) on stream fish communities have been difficult to evaluate given the simultaneous construction of impoundments and conversion of native land covers to human land uses (*sensu* Allan 2004).

The goal of this study was to evaluate the effects of multiple watershed landscape alterations on fish community structure in Great Plains prairie streams of Kansas, USA. Specific objectives included: (i) documenting the number, spatial distribution and size distribution of watershed impoundments in Kansas, (ii) testing the effects of watershed landscape alterations on stream- and impoundment-associated fishes while controlling for the effects of zoogeography and local habitat availability, and (iii) integrating findings into spatial patterns of fish community structure across Kansas. We hypothesised that increased watershed impoundments would positively correlate

with richness of impoundment-associated fishes because of either habitat changes that benefit these fishes or because impoundments themselves serve as source populations (Havel et al. 2005; Johnson et al. 2008). We also hypothesised that watershed impoundments would negatively correlate with richness of stream-associated fishes because of the documented negative effects of impoundments on native stream fishes in the Great Plains (Mammoliti 2002; Gerken & Paukert 2013).

Study area

The state of Kansas is characterised by longitudinal (west to east) gradients in rainfall, elevation and topography. In general, precipitation increases, elevation decreases and topographic complexity increases in an easterly direction. From north to south, the state is bisected by two major river basins, the Kansas River basin to the north and the Arkansas River basin to the south (Fig. 1). Collectively, these gradients in abiotic conditions and biogeographic (drainage basin) boundaries contribute to at least four major fish ecoregions in the state: NW (Kansas River basin, west of the Flint Hills), SW (Arkansas River basin west of the Flint Hills), NE (eastern Kansas River basin) and SE (eastern Arkansas River basin; Hawkes et al.

1986). Overlaid across the longitudinal gradients described above is a west-to-east gradient of increasing numbers of watershed impoundments. Intensive terrestrial landscape changes include conversion of native land cover to row-crop agriculture and urban and suburban land use throughout much of the state (Gido et al. 2010). In other regions, less intensive terrestrial landscape changes include the modification of large herbivore grazing and fire regimes as a consequence of cattle grazing (Larson et al. 2013). These regions include the Flint Hills ecoregion that runs north–south across the state between the −96th and −97th meridians and the Red Hills ecoregion in the south central portion of the state.

Materials and methods

Field methods

Fish community data collected by the Kansas Department of Wildlife, Parks and Tourism (KDWPT) were used in this study. Collections were conducted during May through August 1995–2008 as a part of the KDWPT state-wide Stream Assessment and Monitoring Program. The KDWPT fish community sampling protocol followed that of Lazorchak et al. (1998), with sampling lengths of 40-times the mean wetted
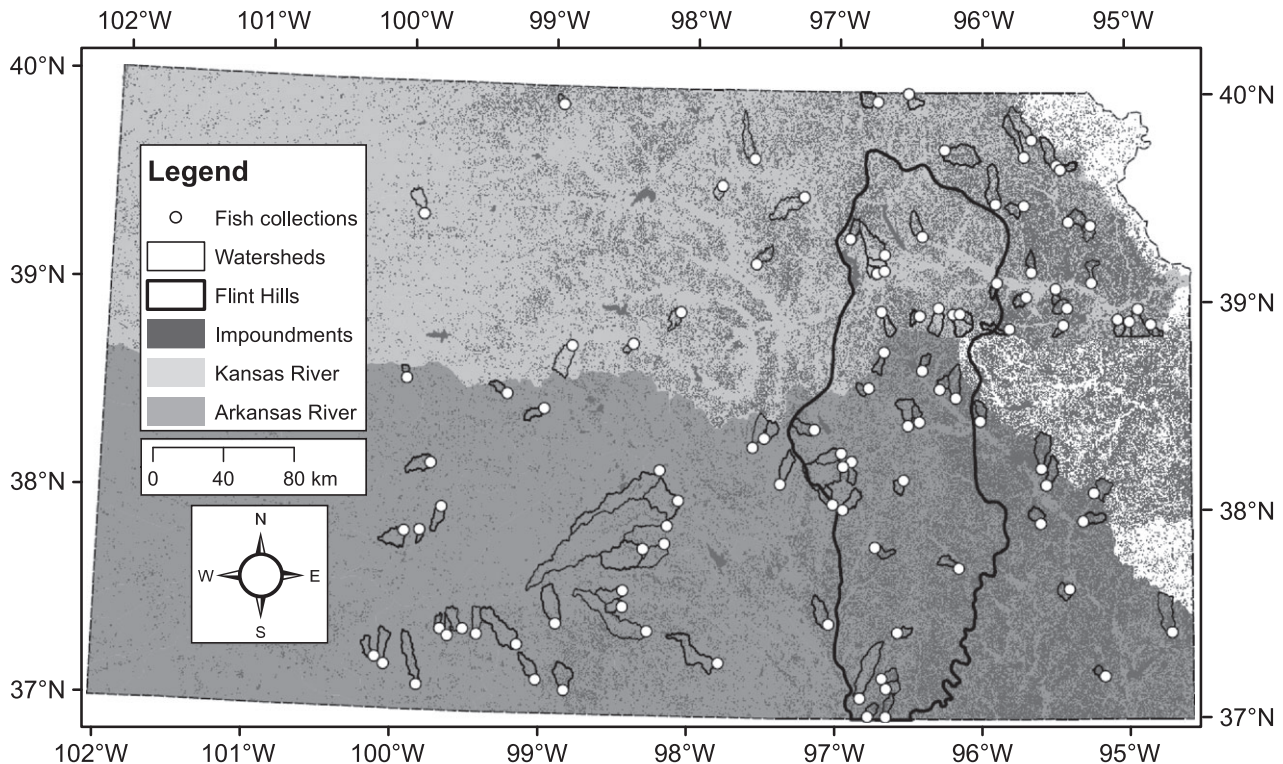

Fig. 1. Locations of stream fish sampling points (open circles) in the Kansas and Arkansas basins of Kansas, USA. Black-filled polygons illustrate impoundments, heavy open polygon is the Flint Hills ecoregion (see text), and open polygons associated with each fish sampling location illustrate watersheds.

width and bounded by lower and upper limits of 150 and 300 m respectively, to ensure representative samples of the community for each site and date. Collections were made using a combination of straight and bag seines (4.7 mm mesh) and DC-pulsed backpack or tote-barge electrofishing. Equal effort among gear types was used for all sites and dates to facilitate comparisons of community structure. Although the KDWPT sampled a variety of wadeable streams, collections used in this study were filtered by stream network position (i.e., Strahler 1957; order = 3rd) because of the strong influence positioning has on fish community structure and species distributions (Thornbrugh & Gido 2010; Troia & Gido 2013). All fishes collected during KDWPT surveying of third-order streams were classified into habitat guilds involving either impoundment or stream habitat associations based on previous indicator species analysis that compared abundance of the different species from standardised sampling of impoundments and streams (Gido et al. 2009). Thus, fishes that were more abundant in impoundment samples were classified as impoundment associates and those more abundant in streams as stream associates.

Three environmental variables representing useful predictors of species richness at a site (local habitat hereafter) were collected by the KDWPT at the time of fish sampling. Survey area was calculated as the total length of stream sampled multiplied by the average stream width measured at 10 evenly spaced transects along the sampling reach. This metric has been used to predict fish species richness at stream sampling sites in and outside of the Great Plains (Fischer & Paukert 2009). Channel width and depth averaged across the same longitudinal transects were also used because of the utility of these metric for predicting fish species richness (Angermeier & Schlosser 1989; Perkin & Gido 2012). These habitat metrics reflect the size of stream habitats available to fishes and are more temporarily stable than related measures such as discharge or velocity and are more useful for predicting species richness regardless of year or season (Gido et al. 2006; Troia & Gido 2013).

Landscape alterations

The primary goal of this study was to evaluate the effects of landscape alterations in the watersheds upstream of fish sampling sites. Watershed delineation for each sampling site was generated from a digital elevation model (DEM, Gesch et al. 2002) through a multistep process using ArcGIS 10 *Hydrology toolbox* (ESRI 2012). Once watersheds were delineated, the number of watershed impoundments within each watershed was calculated based on the

Impoundments shapefile derived from the National Hydrography Dataset Plus (McKay et al. 2012). The total number of impoundments was divided by the area of each watershed polygon to estimate the density of watershed impoundments (# impoundments km^{-2}) upstream of sampling sites. Transformation to intensive terrestrial land use was estimated by calculating the per cent of area in each watershed polygon constituted by agricultural (i.e., row-crop) or urbanised land cover using data from the National Land Cover Database (Fry et al. 2011). This approach generally produces greater predictability than using only buffer zones along the stream corridor (Wang et al. 1997). Although native prairie in several ecoregions (i.e., Flint Hills, Red Hills) is used for cattle grazing, this low intensity land use exerts a lesser impact on in-stream characteristics relative to urban and row-crop land uses and therefore was not included as a terrestrial landscape alteration (Larson et al. 2013). Other forms of landscape alteration exist for Great Plains prairie streams (e.g., woody encroachment, riparian buffer destruction), but these alterations are related to loss of native grassland, which has been subsequently replaced by the major forms of change involving agricultural development, urbanisation and impoundment construction (Dodds et al. 2004; Fischer et al. 2010; Gido et al. 2010).

The first objective of this study was to enumerate watershed impoundments in the state of Kansas to compare with other traditionally quantified forms of landscape change (agriculture, urbanisation). The NHD impoundment layer was used to extract impoundment surface area sizes (km^2) as well as the total number of impoundments within the state. These data were used to construct a histogram of impoundment sizes as well as display the geographic locations of all impoundments. Longitudinal (west to east) patterns in impoundment density and terrestrial landscape alterations involving both urbanisation and agriculture (landscape alteration hereafter) were tested. Given the potential for spatial autocorrelation in landscape features (i.e., sites closer in space might be more similar), relationships were analysed using generalised additive models (GAMs), which account for serial autocorrelation (Wood 2006). Initially, all samples among basins were combined, and basin was treated as a categorical covariate to test for differences in longitudinal patterns in landscape features among the Kansas and Arkansas River basins. When a significant interaction term for basin occurred, separate GAMs were used to describe spatial variation in landscape features for each basin. Relationships between longitude and impoundment density and longitude and terrestrial landscape alterations were analysed and plotted separately. For all GAMs, the *mgcv* package in Program R was used (Wood 2006) and

the central tendency and 95% confidence envelopes displayed.

Structural equation modelling

The second objective of this study was to evaluate the effects of watershed alterations on fish community structure while accounting for the simultaneous effects of zoogeography and the capacity of local habitats to support fishes. Given the complexity of these interactions, a statistical framework capable of incorporating multiple, simultaneous stressors and having the ability to explicitly link ecological processes and spatial patterns was necessary (Bizzi et al. 2013). Structural equation models (SEMs) incorporate direct and indirect effects of stimuli on responses by identifying multiple pathways through which governing mechanisms operate (Burcher et al. 2007). Consequently, an SEM framework was used to develop an *a priori* model useful for describing the potential, interacting effects of geographic location (location hereafter), watershed impounds, landscape alterations, local habitat and fish community structure (Fig. 2). This figure represents a hypothesis by which fish community structure is directly controlled by location (Maloney & Weller 2011), watershed impounds (Mammoliti 2002), landscape alterations (Gerken & Paukert 2013) and local habitat (Gido et al. 2006). Indirect paths controlling fish communities involve the cascading effects of location on watershed impounds, location on landscape alterations and location on local habitat because of the longitudinal gradients that exist across the state of Kansas (as described above). Similarly, watershed impounds and landscape alterations were hypothesised to control local habitat

(DeCoursey 1975; Schoof et al. 1987; Earl & Wood 2002) and indirectly fish community structure. These latent variables were approximated using measured variables described above, including location (measured by longitude), watershed impounds (impoundment density), landscape alterations (per cent urban and agricultural land in watershed), local habitat (survey area, channel width and mean depth) and two measures of fish community response (impoundment-associated and stream-associated species richness).

The *a priori* hypothesised model shown in Fig. 2 was developed into an SEM through model specification (Grace et al. 2010). An initial power analysis was conducted to ensure acceptable sample sizes could be obtained assuming an intermediate (as opposed to weak or strong) effect of landscape alterations on the richness of fishes in surrounding streams (Westland 2010). The assumed intermediate effect size was conservative with respect to the magnitude of effects reported in other studies using SEM frameworks (Burcher et al. 2007; Maloney & Weller 2011). A partial least squares (PLS) SEM approach was utilised because of the relaxed assumptions regarding distributions of the predictor and response variables accommodated by PLS regression. The inner model (containing the latent variables) was parameterised according to the hypothesised governing mechanisms illustrated in Fig. 2. Next, the outer model (containing the measured variables) was parameterised such that longitude was deterministic towards location; impoundment density was deterministic towards watershed impounds; per cent urban and agricultural land uses were deterministic towards landscape alterations; survey area, channel width and mean depth were reflective of local habitat; and
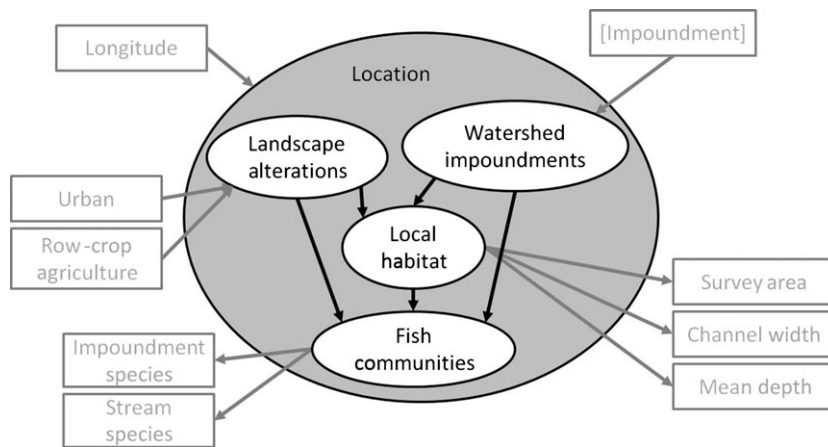

Fig. 2. Conceptual model illustrating the possible pathways through which location, landscape alterations, watershed impounds and local habitat affect stream fish communities in third-order streams of Kansas, USA. Ovals illustrate latent variables and collectively constitute the inner model, and rectangles illustrate manifest (measured) variables that collectively constitute the outer model. Black arrows indicate possible governing mechanisms, and grey arrows indicate causative (pointing towards inner model) and reflective (pointing away from inner model) relationships. Location is shown as an all-encompassing ellipse (location affects everything).

impoundment-associated and stream-associated fish richness were reflective of fish community structure (Fig. 2). Model validation was assessed using a boot-strapping process ($n = 200$ replicates) to determine significance of path coefficients as well as total effects (accounting for direct and indirect effects) of latent variables. Models involving impoundment-associated and stream-associated fishes were specified separately for the Kansas and Arkansas River basins because of documented zoogeographic differences between these basins (Hawkes et al. 1986). All statistical analyses were conducted using the PLS Path Modeling (*plspm*) function in Program R version 2.15 (R Core Development Team 2012). Results were displayed using path diagrams in which significant paths ($P < 0.05$; as determined using bootstrapping) were illustrated with arrow sizes proportional to the path coefficient, correlation coefficients between latent variables were listed along paths and per cent of variation explained by the model at each latent variable shown. The mean and 95% confidence intervals for total effects (direct and indirect) were also shown using bar charts arranged next to path diagrams.

Fish community structure across Kansas

The final objective of this study involved integrating model results into spatial patterns in fish community structure. This objective was achieved by first illustrating the relationship between location (longitude) and fish species richness because the direct effect of location on community composition was significant in all models (Results section). The central tendencies of these relationships were illustrated for impoundment-associated and stream-associated fish species in the Kansas and Arkansas River basins, separately. Given the potential for spatial autocorrelation among sampling sites, GAMs were used to describe spatial variation in species richness for guilds in each basin. A similar GAM approach was used to illustrate the longitudinal convergence of the relative proportion of impoundment-associated and stream-associated fish species (i.e., community structure) across the state of Kansas. This approach allowed for illustrating the spatial context of the SEM outputs to enhance interpretation. Finally, we combined these spatial patterns, the SEM output and known zoogeography of fishes in Kansas to test for the direct interactions between landscape alterations and fish species richness in eastern (i.e., east of the -96.5 meridian) portions of the Kansas (NE fish ecoregion) and Arkansas (SE fish ecoregion) basins. These interactions were tested using generalised linear regression with landscape alteration or watershed impoundment density as the predictor variable and

fish species richness for each guild as the response variable to test for significant slopes after a Bonferroni correction to alpha ($\alpha = 0.05/8 = 0.006$) associated with eight tests (two predictors × two basins × two habitat guilds).

Results

Forty-two-third-order streams were sampled in the Kansas River basin and 62 streams sampled in the Arkansas River basin. These collections spanned a longitudinal gradient across the state from the -100th meridian to approximately the -95th meridian. A total of 67 fish species was reported, including 47 from the Kansas River basin and 64 from the Arkansas River basin. Among the reported fishes, 28 (42%) were classified as impoundment-associated and 39 (58%) were classified as stream-associated (Table 1).

Impoundment densities and landscape alterations varied from west to east and between basins. A total of 182,470 impoundments occurred in Kansas, divided among size classes of surface area ranging from 0.001 to 0.0049 km^2 ($n = 98,191$), 0.005–0.009 km^2 (63,970), 0.01–0.049 km^2 (11,297), 0.05–0.09 km^2 (7,805) and 0.1 to >10 km^2 (1,207). There was no difference in the longitudinal distribution of impoundment densities between the Kansas and Arkansas River basins ($t = 0.218$, $P = 0.83$), so a single GAM was fitted ($F_{2.8,3.4} = 75.6$, $R^2_{adj} = 0.72$, $P < 0.01$). In both basins, watershed impoundment densities averaged <1.0 per km^2 west of the -97th meridian, but increased to over three per km^2 in the eastern portion of the state (Fig. 3a). Longitudinal gradients in terrestrial landscape alterations differed ($t = 3.526$, $P < 0.01$) between the Kansas ($F_{5.8,6.7} = 4.2$, $R^2_{adj} = 0.39$, $P < 0.01$) and Arkansas ($F_{8.2,8.8} = 16.2$, $R^2_{adj} = 0.70$, $P < 0.01$) basins. In general, ~50% of landscapes were altered in both basins west of the -97th meridian; however, per cent of urbanisation plus row-crop agriculture decreased in the vicinity of the Flint Hills ecoregion for both basins before increasing to on-average 80% alteration in the eastern extent of the Kansas River basin and 30% in the eastern extent of the Arkansas River basin (Fig. 3b).

Fitted structural equation models showed similar governing mechanisms for each guild among basins (Table 2). Location governed landscape alterations, watershed impoundments, local habitat and fish communities in the Kansas and Arkansas River basins (Fig. 4). For impoundment-associated fishes in the Kansas River basin, species richness was not governed by landscape alterations or watershed impoundments, but positively correlated with local habitat ($R = 0.56$; total effect = 0.32) so that 54% of varia-

Table 1. Fish species, habitat guild (Imp = impoundment, Str = stream) and occurrence (1 = present) in third-order streams in the Kansas and Arkansas River basins of Kansas, USA.

Genus species	Guild	Kan	Ark	Genus species	Guild	Kan	Ark
Ameiurus melas	Str	1	1	Lythrurus umbratilis	Str	1	1
Ameiurus natalis	Str	1	1	Micropterus punctatus	Imp	1	1
Aplodinotus grunniens	Imp	1	1	Micropterus salmoides	Imp	1	1
Campostoma anomalum	Str	1	1	Minytrema melanops	Imp	–	1
Carassius auritus	Str	–	1	Morone americana	Imp	–	1
Carpiodes carpio	Imp	1	1	Morone chrysops	Imp	1	1
Carpiodes cyprinus	Imp	1	1	Moxostoma erythrurum	Str	1	1
Catostomus commersonii	Str	1	–	Moxostoma macrolepidotum	Str	1	1
Cyprinella camura	Str	–	1	Notropis atherinoides	Imp	–	1
Cyprinus carpio	Imp	1	1	Notropis boops	Str	–	1
Cyprinella lutrensis	Str	1	1	Notemigonus crysoleucas	Imp	1	1
Dorosoma cepedianum	Imp	1	1	Notropis dorsalis	Str	1	–
Etheostoma cragini	Str	–	1	Noturus exilis	Str	1	1
Etheostoma flabellare	Str	–	1	Noturus flavus	Str	1	1
Etheostoma nigrum	Str	1	1	Noturus nocturnus	Str	–	1
Etheostoma spectabile	Str	1	1	Notropis percobromus	Str	1	1
Fundulus kansae	Str	1	1	Notropis stramineus	Str	1	1
Fundulus notatus	Imp	–	1	Notropis topeka	Str	1	1
Gambusia affinis	Str	1	1	Notropis volucellus	Str	–	1
Hybognathus placitus	Str	–	1	Percina caprodes	Imp	1	1
Ictiobus bubalus	Imp	1	1	Percina copelandi	Str	–	1
Ictiobus cyprinus	Imp	–	1	Percina phoxocephala	Str	1	1
Ictalurus punctatus	Str	1	1	Phenacobius mirabilis	Str	1	1
Labidesthes sicculus	Imp	1	1	Phoxinus erythrogaster	Str	1	1
Lepomis cyanellus	Str	1	1	Pimephales notatus	Imp	1	1
Lepomis gulosus	Imp	–	1	Pimephales promelas	Str	1	1
Lepomis humilis	Imp	1	1	Pimephales tenellus	Str	–	1
Lepomis macrochirus	Imp	1	1	Pimephales vigilax	Imp	1	1
Lepomis megalotis	Imp	1	1	Pomoxis annularis	Imp	1	1
Lepisosteus osseus	Imp	1	1	Pomoxis nigromaculatus	Imp	–	1
Lepisosteus platostomus	Imp	–	1	Pylodictis olivaris	Str	1	1

Table 1 *(continued)*

Genus species	Guild	Kan	Ark	Genus species	Guild	Kan	Ark
Luxilus cardinalis	Str	–	1	Sander vitreus	Imp	1	–
Luxilus cornutus	Str	1	1	Semotilus atromaculatus	Str	1	1

tion in richness was explained by the SEM (Fig. 4a). Stream-associated species richness in the Kansas River basin was negatively correlated with landscape alterations ($R = -0.28$, total effect = -0.46), but was not governed by watershed impoundments or local habitat so that 26% of variation in richness was explained (Fig. 4b). Impoundment-associated species richness in the Arkansas River basin was not governed by landscape alterations or watershed impoundments, but was positively correlated with local habitat ($R = 0.30$; total effect = 0.32) so that 46% of variation in richness was explained (Fig. 4c). Stream-associated species richness in the Arkansas River basin was negatively correlated with landscape alterations ($R = -0.21$, total effect = -0.29) and watershed impoundments ($R = 0.03$, total effect = -0.91), but not local habitat so that 39% of variation in richness was explained (Fig. 4d).

Relationships between geographic location and richness illustrated spatial concordance among basins but discordance among guilds. In the Kansas River basin, impoundment-associated fish species generally increased from west to east ($F_{2.0,2.5} = 16.2$, $R^2_{\mathrm{adj}} = 0.49$, $P < 0.01$) so that collections west of the -97th meridian averaged <2 species, but collections east of the -97th meridian steadily increased to on-average seven species (Fig. 5a). For stream-associated species in the Kansas River basin, richness changed through space ($F_{3.8,4.5} = 3.9$, $R^2_{\mathrm{adj}} = 0.28$, $P < 0.01$) and increased from on-average 6–12 in an easterly direction until the -96.5 meridian, east of which richness declined to on-average eight (Fig. 5b). These combined changes in absolute richness in the Kansas River basin contributed to a convergence in the relative proportion of each guild in the eastern extent of the state (Fig. 5c), characterised by a relative decline for stream species ($F_{2.1,2.6} = 13.2$, $R^2_{\mathrm{adj}} = 0.45$, $P < 0.01$) and a relative increase for impoundment species ($F_{2.1,2.6} = 13.2$, $R^2_{\mathrm{adj}} = 0.45$, $P < 0.01$). In the Arkansas River basin, absolute richness of impoundment fish species increased ($F_{2.7,3.3} = 15.8$, $R^2_{\mathrm{adj}} = 0.47$, $P < 0.01$) from west to east from <2 to on-average nine (Fig. 5d) while stream species showed dynamic change ($F_{5.3,6.3} = 11.7$, $R^2_{\mathrm{adj}} = 0.55$, $P < 0.01$) similar to the Kansas River basin (Fig. 5e). Combined
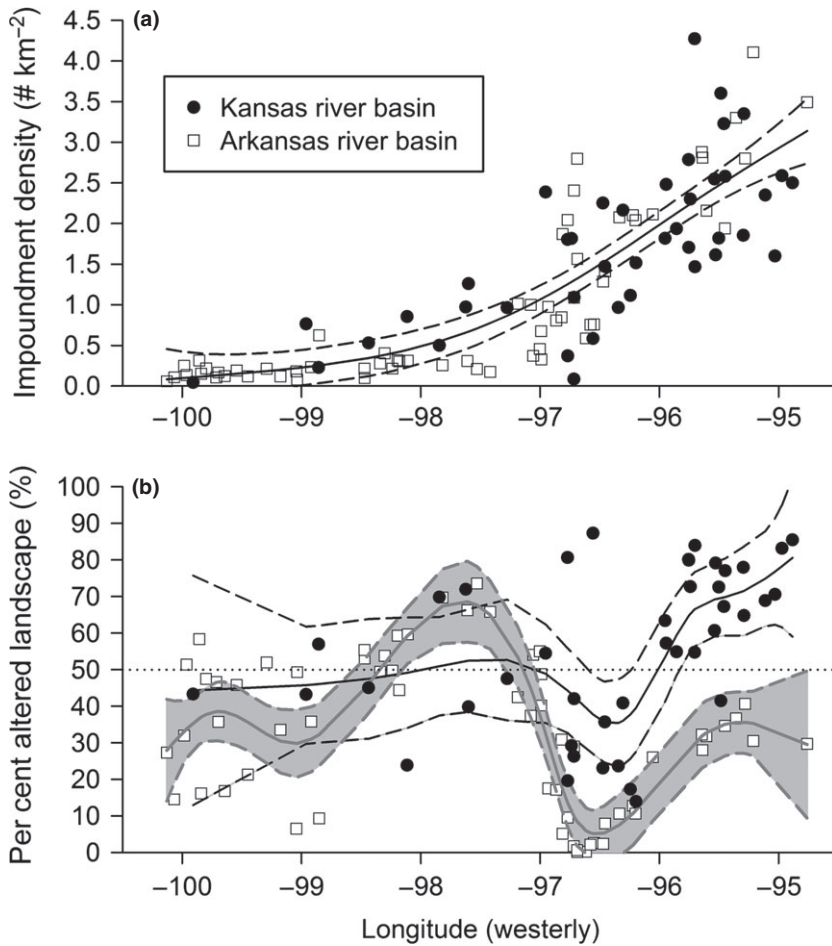
Fig. 3. (a) Longitudinal (west to east) distribution of watershed impoundment densities for third-order streams in the Kansas (filled circles) and Arkansas (open boxes) basins of Kansas, USA, with a single fitted generalised additive model (GAM) illustrating mean (solid line) and 95% confidence intervals (dashed lines). (b) Relationship between longitude and per cent of landscape alterations (per cent agriculture + urbanisation) in watersheds of third-order streams in the Kansas (solid and dashed black GAM) and Arkansas (grey, shaded GAM) basins of Kansas, USA. The dotted line represents the 50% mark.

Table 2. Path coefficients, total effects (direct and indirect), and upper and lower bootstrapped confidence envelopes for geographic location (Loc), watershed impoundments (Imp), terrestrial landscape alterations (Land), habitat capacity (Hab), and fish community structure (Com) components of structural equation models fitted for impoundment and stream fish species in the Kansas and Arkansas River basins of Kansas, USA. Bolded values indicated envelopes that do not include zero (i.e., significant).

|	Impoundment species						Stream species					
	Path coefficients			Total effects			Path coefficients			Total effects		
Variables	Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper
Kansas River basin												
Loc → Imp	**0.71**	**0.57**	**0.82**	**0.71**	**0.57**	**0.82**	**0.71**	**0.61**	**0.81**	**0.71**	**0.61**	**0.81**
Loc → Land	**0.44**	**0.29**	**0.60**	**0.44**	**0.29**	**0.60**	**0.45**	**0.29**	**0.60**	**0.45**	**0.29**	**0.60**
Loc → Hab	**0.71**	**0.38**	**1.01**	**0.48**	**0.27**	**0.65**	**0.72**	**0.42**	**1.06**	**0.48**	**0.30**	**0.63**
Loc → Com	**0.47**	**0.05**	**0.78**	**0.68**	**0.54**	**0.80**	0.47	−0.04	0.95	0.22	−0.06	0.50
Imp → Hab	−0.29	−0.65	0.02	−0.29	−0.65	0.02	**−0.29**	**−0.60**	**−0.01**	**−0.29**	**−0.60**	**−0.01**
Imp → Com	0.10	−0.21	0.38	0.00	−0.32	0.29	−0.17	−0.68	0.41	−0.21	−0.69	0.29
Land → Hab	−0.06	−0.40	0.25	−0.06	−0.40	0.25	−0.08	−0.47	0.30	−0.08	−0.47	0.30
Land → Com	−0.03	−0.26	0.28	−0.05	−0.31	0.25	**−0.45**	**−0.74**	**−0.21**	**−0.46**	**−0.76**	**−0.19**
Hab → Com	**0.32**	**0.06**	**0.56**	**0.32**	**0.06**	**0.56**	0.16	−0.25	0.54	0.16	−0.25	0.54
Arkansas River basin												
Loc → Imp	**0.81**	**0.75**	**0.87**	**0.81**	**0.75**	**0.87**	**0.81**	**0.74**	**0.86**	**0.81**	**0.74**	**0.86**
Loc → Land	**−0.27**	**−0.45**	**0.00**	**−0.27**	**−0.45**	**0.00**	**−0.27**	**−0.48**	**−0.06**	**−0.27**	**−0.48**	**−0.06**
Loc → Hab	**0.70**	**0.41**	**0.95**	**0.53**	**0.35**	**0.72**	**0.69**	**0.38**	**0.94**	**0.53**	**0.37**	**0.72**
Loc → Com	**0.49**	**0.09**	**0.81**	**0.59**	**0.45**	**0.74**	**0.97**	**0.49**	**1.33**	**0.35**	**0.09**	**0.62**
Imp → Hab	−0.22	−0.54	0.10	−0.22	−0.54	0.10	−0.21	−0.55	0.11	−0.21	−0.55	0.11
Imp → Com	−0.14	−0.57	0.41	−0.21	−0.66	0.35	**−0.90**	**−1.31**	**−0.51**	**−0.91**	**−1.31**	**−0.52**
Land → Hab	−0.08	−0.33	0.12	−0.08	−0.33	0.12	−0.05	−0.28	0.18	−0.05	−0.28	0.18
Land → Com	−0.17	−0.34	0.06	−0.20	−0.41	0.07	**−0.29**	**−0.45**	**−0.02**	**−0.29**	**−0.46**	**−0.02**
Hab → Com	**0.32**	**0.04**	**0.57**	**0.32**	**0.04**	**0.57**	0.05	−0.18	0.38	0.05	−0.18	0.38
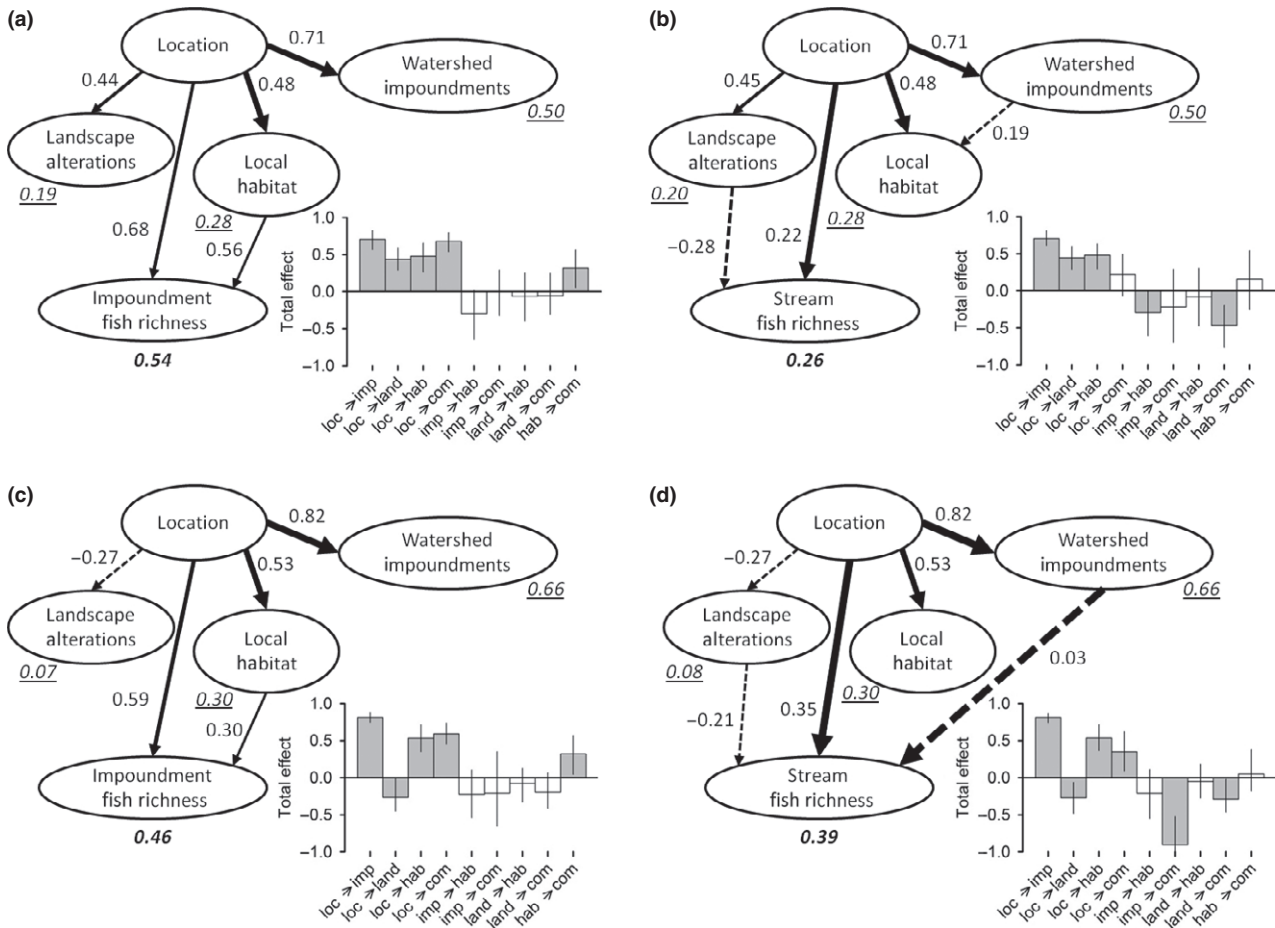
Fig. 4. Fitted structural equation diagrams illustrating relationships between location (loc), watershed impoundment density (imp), landscape alterations (land), habitat capacity (hab) and fish community structure (com) for impoundment-associated (left panels) and stream-associated (right panels) fishes in the Kansas (upper panels) and Arkansas (lower panels) basins of Kansas, USA. Black lines indicate significant ($P < 0.05$) positive (solid) and negative (dashed) path coefficients among latent variables. Arrow thickness indicates the strength of the effect for the relationship, values next to arrows indicate correlation coefficients, and underlined values near latent variables represent the amount of variation explained by the proceeding portion of the model. Bolded values near responses indicated the amount of variation in species richness explained by the model. Insert bar charts illustrate mean (±95% confidence interval) total effects (direct and indirect) determined through bootstrapping ($n = 200$) and illustrate significant (grey bars) and non-significant (white bars) effects.

changes in guild richness for the Arkansas River basin contributed to an inversion of dominance in the eastern portion of the state (Fig. 5f), characterised by a general decline of stream species ($F_{5.6,6.7} = 5.5$, $R^2_{adj} = 0.37$, $P < 0.01$) and relative increase of impoundment species ($F_{5.6,6.7}$ 5.5, $R^2_{adj} = 0.37$, $P < 0.01$). Convergence in the relative proportions of guilds was related to negative relationships between landscape features and stream fish richness in the eastern fish ecoregions but no relationship between landscape features and impoundment fish richness (Table 3). In eastern Kansas, per cent of altered landscape predicted significant decline of stream fish richness ($F_{1,24} = 5.54$, $P = 0.03$, $R^2 = 0.19$) in the Kansas River basin (Fig. 6a) and watershed impoundment density predicted significant decline in stream fish richness ($F_{1,10} = 21.53$, $P < 0.01$, $R^2 = 0.68$) in the Arkansas River basin (Fig. 6b).

Discussion

Environmental drivers of richness

Richness of stream-associated and impoundment-associated species was influenced by multiple independent and interactive environmental factors. Location was directly associated with richness of impoundment and stream species and was consistent across basins. This is likely related to historical and contemporary fish distributions in Kansas (Hawkes et al. 1986) and could result from two possible mechanisms. First, neutral metacommunity models predict higher species richness with increasing mean annual run-off apparent in eastern Kansas relative to western Kansas (Muneepeerakul et al. 2008). Although our analysis did not directly measure run-off, inclusion of location in our models indirectly captured this pattern
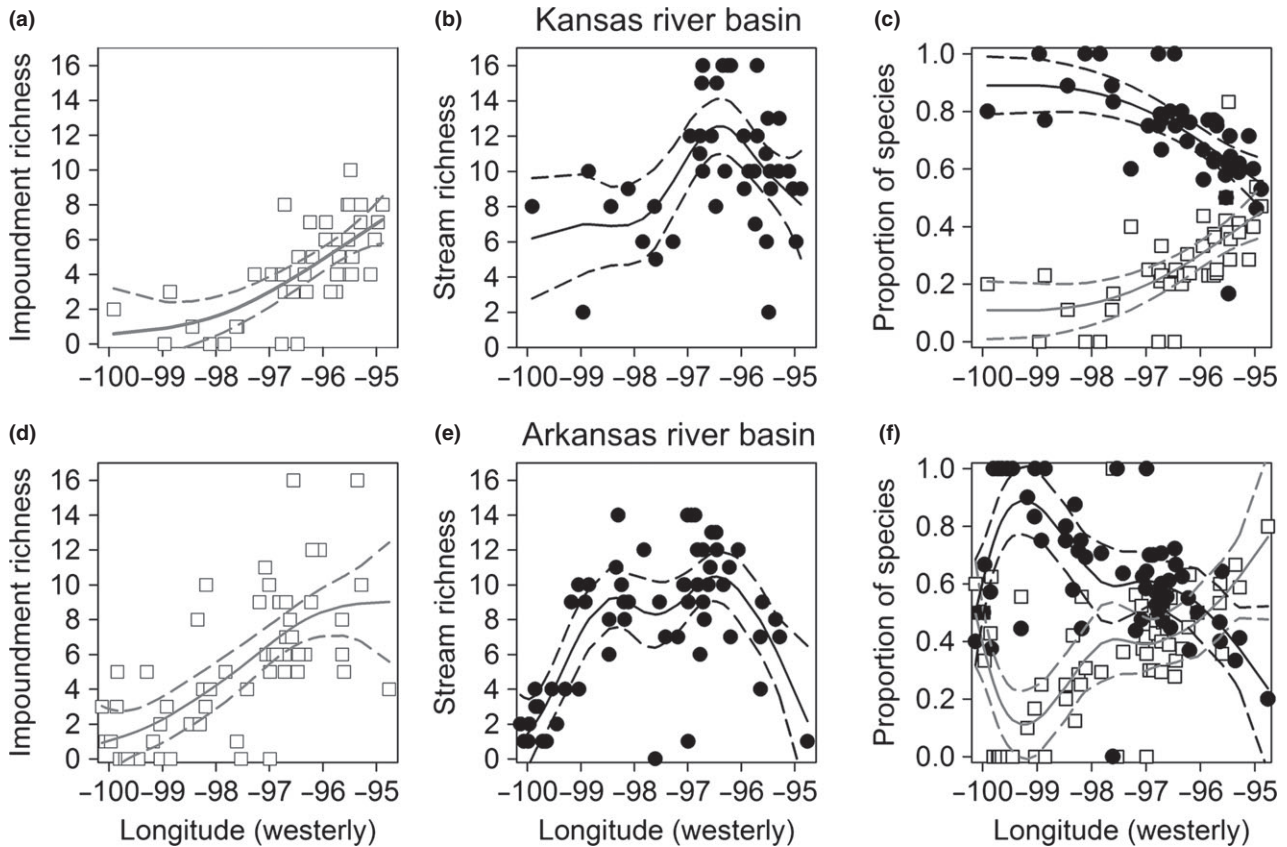
Fig. 5. Relationship between longitude and impoundment species richness, stream-species richness, and the relative proportion of species belonging to each guild for the Kansas (upper panels) and Arkansas (lower panels) basins of Kansas, USA. Regression lines are fitted generalised additive models and illustrate the central tendency (solid line) and 95% confidence intervals (dashed lines).

Table 3. General linear regression models for the relationship between landscape alterations (per cent row-crop agriculture + urbanisation) or watershed impounds (# km^{-2}) and impoundment-associated or stream-associated fish species richness for Great Plains prairie streams in the Kansas and Arkansas River basins of Kansas, USA.

Kansas River basin	$F_{1,24}$	P-value	R^2
Impoundment fish richness			
Landscape alterations	1.24	0.28	0.05
Watershed impounds	0.72	0.41	0.03
Stream fish richness			
Landscape alterations	5.54	0.03	0.19
Watershed impounds	2.39	0.14	0.09
Arkansas River basin	$F_{1,10}$	P-value	R^2
Impoundment fish richness			
Landscape alterations	0.96	0.35	0.09
Watershed impounds	0.62	0.45	0.06
Stream fish richness			
Landscape alterations	4.49	0.06	0.31
Watershed impounds	21.53	<0.01	0.68

as with other SEM approaches that include location as a master variable (Maloney & Weller 2011). We consider run-off to be outside of the focus of our landscape analysis given that our specific objectives were related to structures on the landscape which themselves are linked to rainfall. This is the basis for the second mechanism by which our models suffered from unexplained variation related to location. Environmental conditions not captured by the intermediate latent variables in our SEM (i.e., land cover or local habitat) such as substrate composition, width-to-depth ratio, large wood, and the quantity and origin of basal food resources are known to vary from east to west in Kansas and probably affect the composition of fish communities (Troia & Gido 2013). Location also governed richness of impoundment species indirectly through local habitat. The increase in habitat capacity from west to east is likely a consequence of natural and anthropogenic gradients, including higher precipitation in the east and extensive groundwater pumping in the west (Gido et al. 2010; Perkin et al. 2014). Similarly, Falke & Gido (2006) observed that impoundment-associated species were most abundant in larger pools of a fourth-order stream flowing directly into a large Kansas River basin reservoir, consistent with greater impoundment species richness in habitats with greater capacity to support these fishes. Our study provides more refined information on impoundment-associated species by documenting
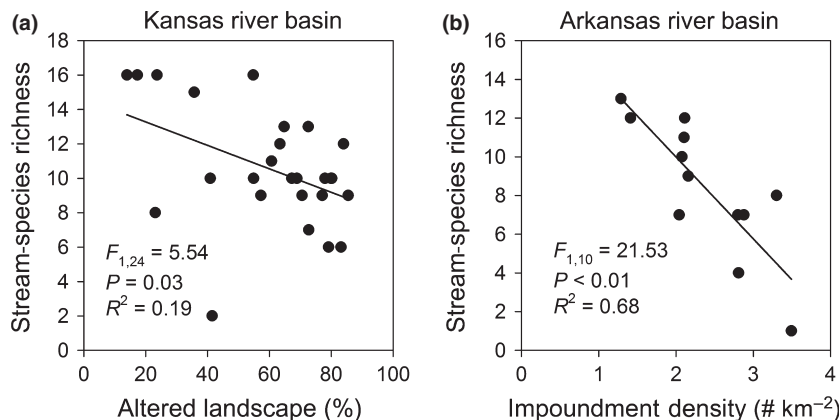
Fig. 6. Relationship between (a) per cent altered landscape and stream fish species richness in the Kansas River basin and (b) impoundment density and stream fish species richness in the Arkansas River basin of Kansas, USA.

the prevalence of the relationship between impoundment fishes and suitable habitats across most streams in the Kansas and Arkansas River basins. Furthermore, our findings suggest this pattern is not limited to the larger streams studied by Falke & Gido (2006) and that it is also prevalent in headwater streams that are not necessarily in close proximity to large reservoirs.

Local habitat capacity was not related to richness of stream-associated fishes. This lack of governance could be a direct consequence of isolation or disturbance history, or indirectly as a consequence of predation by the numerous impoundment-associated piscivores that typically occupy large pools in headwater streams (Schlosser 1987; Creed 2006). In terms of disturbance history, failure of SEMs to detect an interaction between stream-associated richness and local and landscape features might be related to past declines and extirpations of many stream fishes in the state (Mammoliti 2002; Haslouer et al. 2005; Gido et al. 2010). By this account, our analysis of spatial patterns in contemporary (i.e., post 1994) fish distributions was biased towards species that have largely resisted landscape alterations that now affect a large extent of the Great Plains (Hoagstrom et al. 2011). These findings highlight the importance of synthesising studies that document long-term temporal community change with studies of contemporary spatial variation in community composition. In terms of indirect predation effects, the abundance and occurrence of piscivorous impoundment-associated fishes have increased over the past half century (Gido et al. 2010). Increases among these fishes are implicated in the ongoing decline of stream fishes (Schrank et al. 2001; Gerken & Paukert 2013) and cannot be ruled out as contributing to the observed patterns in this study.

Although urban and agricultural land use correlated with location, these terrestrial landscape alterations did not affect impoundment-associated species richness. Indeed, even in the eastern portion of the

Kansas River basin where terrestrial land alteration is widespread, impoundment-associated species were still prevalent. By contrast, terrestrial landscape modifications negatively affected the richness of stream-associated species, although the causal paths differed between the Kansas and Arkansas River basins. Because terrestrial landscape alterations are most abundant in the eastern Kansas River basin, the negative impact of these terrestrial landscape alterations was most prevalent in the eastern portion of that basin as might be expected given established linkages between landscapes and stream communities (Likens et al. 1978; Maloney & Weller 2011). This was apparent in the SEM output, in which location indirectly affected stream-associated species richness via an intermediate path with terrestrial landscape alteration. In the Arkansas River basin, terrestrial landscape alterations were not strongly correlated with geographic location (although the total effect was negative), which is consistent with reduced terrestrial landscape alterations in the eastern extent of the Arkansas River basin. Although terrestrial landscape alterations were less intense in the eastern Arkansas River basin, a negative effect on stream-associated fishes was apparent as expected under the LCC framework (Burcher et al. 2007). Interestingly, watershed impoundments had a stronger negative effect on stream-species richness in the eastern Arkansas River basin (relative to terrestrial alterations) as predicted based on previous work at finer spatial extents (Schrank et al. 2001; Mammoliti 2002; Gerken & Paukert 2013). This pattern suggests watershed impoundments represent a threat to stream fish diversity in relatively pristine watersheds that are not heavily afflicted by more traditionally recognised forms of landscape alteration (e.g., forest removal or agricultural development, Richards et al. 1996; Wang et al. 1997). This finding extends our understanding beyond human-dominated landscapes contributing to degraded stream ecosystems via only terrestrial changes to include the contribution of watershed

impoundments towards the ongoing decline of stream fishes that lack tolerant or generalist traits (Poff & Allan 1995).

Impoundments facilitating invasion

Density of watershed impoundments was not correlated with richness of impoundment-associated species in either basin. We hypothesised that these impoundments would increase the richness of impoundment species indirectly by altering flow regimes and channel morphologies to favour impoundment species or directly by contributing propagules. This finding is in spite of watershed impoundments such as those included in this study being stocked annually with >2.5 billion fishes across North America (Heidinger 1999; Dauwalter & Jackson 2005) and individuals frequently washing out through overflow structures (Flickinger et al. 1999). Although propagules can disperse through altered hydrologic connections to sustain or supplement fish communities (Woodford et al. 2013), our correlative approach found no evidence of such connection. This is most likely an artefact of our use of species occurrence (i.e., binary) as a response variable rather than density or abundance (i.e., continuous), two measures that would be more sensitive to propagule supplementation given that occurrence of only a single individual informs species richness. Further, watershed impoundments are known to contribute to narrower and shallower channels with finer substrates (Friedman et al. 1998; Earl & Wood 2002), and these habitat modifications would tend to reduce habitat capacity for impoundment species as measured in our study. Evidence for this interaction was illustrated by the negative, but not significant, total effect of watershed impoundments on habitat capacity for impoundment-associated fish species SEMs in both basins. Instead, we found that impoundment-associated species richness increased in an easterly direction as related to local habitat and is largely unrelated to landscape alterations. Thus, although large impoundments are associated with fish invasions in the Great Plains (Gido et al. 2004), additional research directly testing for the dispersal of adults or propagules from impoundments into surrounding streams is necessary to evaluate any increased invasion potential caused by watershed impoundments.

Broader context

Structural equation models provide a useful approach for integrating existing conceptual models of community assembly in hierarchically structured (dendritic) ecological networks. The metacommunity concept posits that local community composition may be influenced by a combination of local (e.g., niche filtering) and regional (e.g., dispersal among localities) processes (Leibold et al. 2004). Our findings suggest that niche filtering imposes an overriding influence on the composition of prairie stream fish communities in Kansas. Local environmental conditions (i.e., stream width, depth, area) associated with catchment land use and geographic location influenced community composition likely by differentially filtering impoundment-associated and stream-associated community members. By contrast, our SEMs did not indicate a direct positive effect of impoundment density on the richness of impoundment-associated fishes, suggesting that impoundment species do not disperse in large numbers from upstream impoundments into sampling sites. Although movement of fishes from small impoundments to streams does not appear to contribute to community assembly in prairie streams, such mass effects (*sensu* Leibold et al. 2004) can be important drivers of community composition in these same prairie streams in other contexts. For example, Perkin & Gido (2012) showed that headwater stream fish communities are altered when isolated from adjacent stream reaches by perched road crossings. In this context, stream-associated fishes with greater dispersal affinities were most afflicted by fragmentation, suggesting that habitat associations might determine, at least in part, species response to hydrologic connectivity (Perkin et al. 2013). If stream-associated fishes require greater habitat and hydrologic connectivity, then fragmentation of this connectivity might constitute an additional pathway through which watershed impoundments imperil stream fishes (Gerken & Paukert 2013). This hypothesis might be tested by measuring and comparing the dispersal affinities and habitat associations of stream-associated and impoundment-associated fishes (Gido et al. 2009).

Dendritic ecological networks are unique among other landscape types in that local habitat characteristics are a consequence of hierarchically structured stream habitat (Campbell Grant et al. 2007), whereby environmental characteristics of the upstream catchment constrain in stream habitat (Frissell et al. 1986; Burcher et al. 2007). Studies from a variety of regions have demonstrated this through frameworks such as the LCC (Burcher et al. 2007), although the stimuli for change within streams generally include terrestrial land cover change (Likens et al. 1978; Richards et al. 1996; Wang et al. 1997; Maloney & Weller 2011). However, in addition to terrestrial landscape modification affecting local habitat characteristics, our study highlights the potential for coincident watershed impoundments to negatively govern the distribution of some stream fishes. The SEM framework provides an effective means to characte-

rise the relative contribution of local and regional processes to community assembly by simultaneously evaluating correlations among catchment land cover, in-stream conditions, upstream impoundment density and community composition. In summary, the constraints that formerly plagued our ability to assess how multiple, interacting landscape alterations influence stream ecosystems (see Allan 2004) have largely been addressed by advancing application of SEM frameworks to ecological problems (Bizzi et al. 2013).

Conclusion

Prairie stream fish communities have undergone drastic change in the past century as a consequence of broad-scale human alteration of Great Plains landscapes (Gido et al. 2010; Perkin et al. 2014). Previous studies have revealed a variety of mechanisms by which such change has occurred including groundwater extraction (Falke et al. 2010), construction of large impoundments on river main stems (Falke & Gido 2006), conversion of native prairie to human land uses (Gerken & Paukert 2013) and fragmentation of hydrologic connectivity in headwater stream reaches by road crossings (Perkin & Gido 2012). Despite these established relationships, some landscape-scale threats to stream fishes are routinely overlooked (Utz 2014). The current study provides a test of the effects of a previously unevaluated type of landscape modification (watershed impoundment construction) that is prevalent throughout most regions of the world (Lehner et al. 2011). It is important to consider the context dependencies of species-environment relationships, particularly when performing analyses at broad spatial extents where relatively long gradients (e.g., geographic location) might influence the relationships observed between biota and the relatively short environmental gradients (e.g., local habitat or land cover) that are nested within (Maloney & Weller 2011). In this study, although impoundment-associated fish richness increased from west to east across the entire extent of the state, the convergence of relatively equal numbers of impoundment and stream species in the eastern extent of the state was actually related to the negative relationship between landscape modifications (development + impoundments) and stream-associated fish richness. Thus, our study highlights effects of previously documented mechanisms responsible for transferring land-cover-disturbances to stream biota (e.g., agricultural or urban land development; Burcher et al. 2007) and provides new evidence for the largely ignored effects of watershed impoundments on stream fish community structure.

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