ORIGINAL ARTICLE

Freshwater Biology WILEY

Fish assemblage composition within the floodplain habitat mosaic of a tropical lake (Tonle Sap, Cambodia)

Thomas Pool[1,2] (ID) | Vittoria Elliott[3] | Gordon Holtgrieve[1] | Mauricio Arias[4] | Irit Altman[5] | Leslie Kaufman[5] | Kevin McCann[6] | Evan D. G. Fraser[7] | Loïc Tudesque[8] | Mathieu Chevalier[8] | Gael Grenouillet[8] | Ratha Chea[8] | Sovan Lek[8] | Bailey McMeans[9] | Michael Cooperman[10] | Chheng Phen[3] | Lee Hannah[11] | Ben Miller[1] | Chuanbo Guo[12] (ID) | So Nam[12]

[1]School of Aquatic and Fishery Sciences (SAFS), University of Washington, Seattle, WA, U.S.A

[2]Biology Department, Seattle University, Seattle, WA, U.S.A

[3]Inland Fisheries Research and Development Institute (IFReDI), Fisheries Administration, Phnom Penh, Cambodia

[4]Department of Civil and Environmental Engineering, University of South Florida, Tampa, FL, U.S.A

[5]Biology Department, Boston University, Boston, MA, U.S.A

[6]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

[7]Department of Environmental Sciences, University of Guelph, Guelph, Ontario, Canada

[8]CNRS, Université Toulouse III Paul Sabatier, ENFA, Laboratoire Évolution & Diversité Biologique, Toulouse, France

[9]Department of Biology, University of Toronto, Mississauga, Ontario, Canada

[10]Conservation International's Center for Applied Biodiversity, Arlington, TX, U.S.A

[11]Bren School of Environmental Science and Management, University of California, Santa Barbara, CA, U.S.A

[12]Mekong River Commission, Phnom Penh, Cambodia

Correspondence
Thomas Pool, Biology Department, Seattle University, 901 12th Avenue, Seattle, WA 98122, U.S.A.
Email: poolt@seattleu.edu

Funding information
John D. and Catherine T. MacArthur Foundation; Margaret A. Cargill Foundation; European Union; National Science Foundation, Grant/Award Number: DEB-1541694 and EAR 1740042; Natural Science and Engineering Research Council

Abstract

1. Understanding how habitat heterogeneity is linked to biodiversity patterns within flood–pulse catchments is needed for their effective conservation. To study those communities, researchers have begun to explore how local environmental factors influence species composition patterns at relatively fine scales within complex habitat mosaics. However, a robust description of the link between communities' composition and their floodplain habitat characteristics remains poorly articulated.

2. In the Tonle Sap Lake (TSL) of Cambodia, we evaluated whether mesohabitat-scale (1–5 km) factors throughout the floodplain structured the fish assemblage temporally and spatially. First, we determined whether TSL fish assemblage changed seasonally and, if so, what assemblage components were driving that change. Second, we determined whether environmental factors structured fish composition across floodplain mesohabitat patches during the wet season. Third, we evaluated whether dominant species displayed affinities for specific areas within the floodplain during the wet season, potentially identifying critical mesohabitat patches for the fish assemblage.

3. Fish were collected from nine sites along an elevational gradient traversing the floodplain every 3 months from March 2014 through January 2015. Correspondence analysis and analysis of variance were used to assess seasonal variation in the species composition. Canonical correspondence analysis and a mantel test were then used to identify the significance of environmental factors structuring the fish assemblage.

4. Fish assemblages changed across seasons; in particular, migratory species occurrence decreased during the dry season. During the wet season, the fish assemblage was structured spatially by mesohabitat-scale factors such as vegetation and water quality. Furthermore, the flooded forest mesohabitat directly adjacent to the permanent lake displayed particularly high species richness and abundance. However, a majority of TSL species appeared to be highly mobile, occurring across multiple floodplain mesohabitats.

5. We concluded that fish assemblage structure and floodplain mesohabitat use within TSL may depend strongly upon the maintenance of the natural flow regime. Since the flow regime will probably be modified by upstream dam development, trade-offs will emerge between the cycle of fishing on which local residents depend, and the hydropower and agricultural benefits of damming the Mekong River system.

1 | INTRODUCTION

Flood–pulse aquatic systems regularly inundate terrestrial landscapes, extensively increasing those systems' habitat complexity and resource availability (Junk, Bayley, & Sparks, 1989). In flood–pulse networks that experience periods of sustained seasonal inundation (e.g. the Amazon and Mekong River basins), dramatic changes in ecosystem size and functioning can also occur (Wantzen, Junk, & Rothhaupt, 2008). For example, substantial shifts in the edge of the freshwater littoral zone have been associated with increased primary production and decomposition rates (Jardine et al., 2015), presumably associated with a diverse array of energy transfer pathways within floodplain food webs (Goulding, 1980; Robinson, Tockner, & Ward, 2002). Unfortunately, despite recognition that floodplains are heterogenous landscapes, we still do not clearly understand how mesohabitat-scale factors (i.e. a combination of distinct vegetation types and water quality elements across metre to kilometre distances; Wilkes, Maddock, Link, & Habit, 2016) influence food web structure in flood–pulse environments.

In floodplain systems, water dynamics appear to be a primary driver influencing vegetation (e.g. inundated gallery forest, lowland shrubland, or grasslands; Worbes, 1985; Valle Ferreira & Stohlgren, 1999; Parolin et al., 2004; Foti, del Jesus, Rinaldo, & Rodriguez-Iturbe, 2012; Arias, Cochrane, Norton, Killeen, & Khon, 2013;

Arias, Wittmann, Parolin, Murray-Hudson, & Cochrane, 2018) and physiochemical characteristics (e.g. dissolved oxygen, pH, and conductivity; Röpke, Ferreira, & Zuanon, 2014). During the wet season, when water levels are at their peak, such patch variation may be particularly important in shaping food web structure and species composition at the mesoscale (Schindler & Scheuerell, 2002; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). For example, many fishes in flood–pulse lakes are known to engage in lateral migrations from open water into inundated landscape habitats during seasonal flooding events, satisfying several life-history demands, such as foraging on newly accessible resources (i.e. submerged plant matter; Fernandes, 1997) and seeking spawning habitat (Godinho, Lamas, & Godinho, 2010). Shifts in fishes' mesohabitat use are significant because they can strongly influence the trophic interactions of entire food webs (Carpenter & Kitchell, 1993), nutrient cycling (Vanni, 2002), primary productivity (Schindler, Carpenter, Cole, Kitchell, & Pace, 1997), and fisheries production. However, understanding how the habitat template influences the spatial intricacies of food web structure is challenging because of the persistent movement of fishes within these systems (Castello, 2008), seasonally reshuffling species and their food web relationships. Nevertheless, it has also been hypothesised that fish in flood–pulse lake systems may associate with specific mesohabitats during the wet season, displaying fine-scale niche partitioning within floodplains (Wood & Bain, 1995).

Exploring the association between floodplain structure and fish assemblages has critical conservation implications at a global scale. This is because most flood–pulse systems are hotspots for regional biodiversity, in addition to having cultural, nutritional, and economic value for millions of people (Keskinen et al., 2013). For example, in the Tonle Sap Lake (TSL) and its tributaries in central Cambodia, 79% of the annual fish catch comes from the freshwater fisheries, 80% of the country's protein is derived directly or indirectly (as a juvenile nursery) from TSL, and approximately 80% of the Cambodian people depend on a combination of fish production and small-scale agriculture for their livelihoods (Bonheur & Lane, 2002; Hortle, 2007). Regrettably, preliminary exploration indicates that flood–pulse systems are experiencing significant pressure associated with habitat loss and flow regime change around the world, due largely to dam development and climate change. As such, it is essential to study the food web structure within flood–pulse systems in order to predict how anthropogenic drivers will impact those systems in the future.

In this study, we investigate how the TSL fish assemblage composition varies across floodplain mesohabitats and seasons. Despite advances in our understanding of TSL hydro-ecological processes, including trophic interactions (Pool et al., 2017), flood pulse dynamics (Arias et al., 2013), and energy transfer (Costa-Cabral et al., 2008; Holtgrieve et al., 2013) at the whole system scale, interactions among the lake's hydrology, floodplain mesohabitats and food web structure remain largely unexplored. Thus, we investigate fishes' taxonomic patterns within the TSL and identify how their life-history characteristics underpin those patterns within the complex floodplain environment. First, we assess the manner in which fish assemblage richness and abundance changes seasonally and identify the primary drivers of composition change over time. We predict that substantial changes in the fish assemblage occur seasonally, driven primarily by the increased presence of migratory species into the TSL during the wet season. Second, we explore how environmental factors structure fish species composition across mesohabitat patches during the wet season, the sampling period with the maximum diversity of inundated habitats. We predict that variation in water parameters and habitat features will define fish species' mesohabitat associations, influenced in large part by species' life-history requirements (i.e. demersal or pelagic species habitat and foraging requirements). Third, we explore if dominant species within the system display affinities for particular areas within the floodplain, along a gradient of inundation duration. We predict that pelagic species will display affinities for deeper regions of the floodplain with demersal species being more common in shallower waters. Furthermore, we anticipate that piscivores will tend to associate with deeper water mesohabitats directly adjacent to the perennially open lake environment while omnivores and herbivores will seek refuge and foraging opportunities in shallower floodplain waters. Taken together, this study provides insight into how floodplain mesohabitat homogenization may impact regional sustainability of fisheries throughout TSL.

2 | METHODS

2.1 | Field design and sampling

Sites (n = 9) were identified along an elevational and hydrological gradient traversing the TSL floodplain in the Pursat province of Cambodia, and were sampled every three months from March 2014 through January 2015 (Figure 1; Arias et al., 2012). Given that the sites were oriented perpendicular to the lake edge, the sites created a floodplain cross-section of inundation-dependent sampling locations, from deep open water mesohabitat (site 1) to shallow lake fringe mesohabitat (site 9). The waterline (or *leading edge*) seasonally shifts *c.* 12 km into the floodplain as the lake's maximum depth increases from *c.* 1 to *c.* 9 m, thus not all sites were submerged throughout the flood–pulse cycle. All nine sites were submerged in September (i.e. the maximum inundation point during the wet season), three sites were submerged during January and March (sites 1, 2, and 3, with the other six sites being dry land), and only two sites were submerged during the dry season in June (sites 1 and 2). This sampling approach captured the lowest (June) and highest (September) water periods of the flood–pulse cycle for that year. This amount of sampling effort provided a balance between accurately identifying composition patterns while minimising the sacrifice of animals for our study. The Inland Fisheries Research and Development Institute (IFReDI) approved our sampling protocol and we followed their conservation and ethics guidelines during our study.

To study fish assemblage and environmental variability throughout the floodplain, we sampled at each submerged site during every sampling event. To study the fishes, two multi-panel gill nets were deployed at every site. Those nets contained five different mesh sizes (10, 20, 30, 50, and 75 mm, with each individual mesh panel being 1 × 1 m). This effectively targeted a wide range of fish species and sizes. The nets were set in coordination with local fishermen for 14–16 hrs, after which the catch was identified to the species level. The standard length of each specimen was measured to the nearest millimetre to determine if within-species size variation occurred between sites. However, despite our best efforts, we certainly did not collect representatives from all species occurring within our study area. Regardless, the species that dominate the catch within the TSL, along with representatives from most families, were captured during our study, giving us confidence in our overall sampling design.

Surface water environmental variables were recorded at each site, including dissolved oxygen (DO; mg/L), pH, temperature, conductivity, total depth, and secchi depth. A single measurement was taken for each environmental variable at the specific location the nets were deployed. Additional vegetation data collected at the same sites were taken from Arias et al. (2013), including vegetation type, canopy cover (%), and understory cover (%). Vegetation data from Arias et al. (2013) reflect multi-decadal successional processes at the site level and are unlikely to have changed over the intervening time period between our two studies (Table S1).
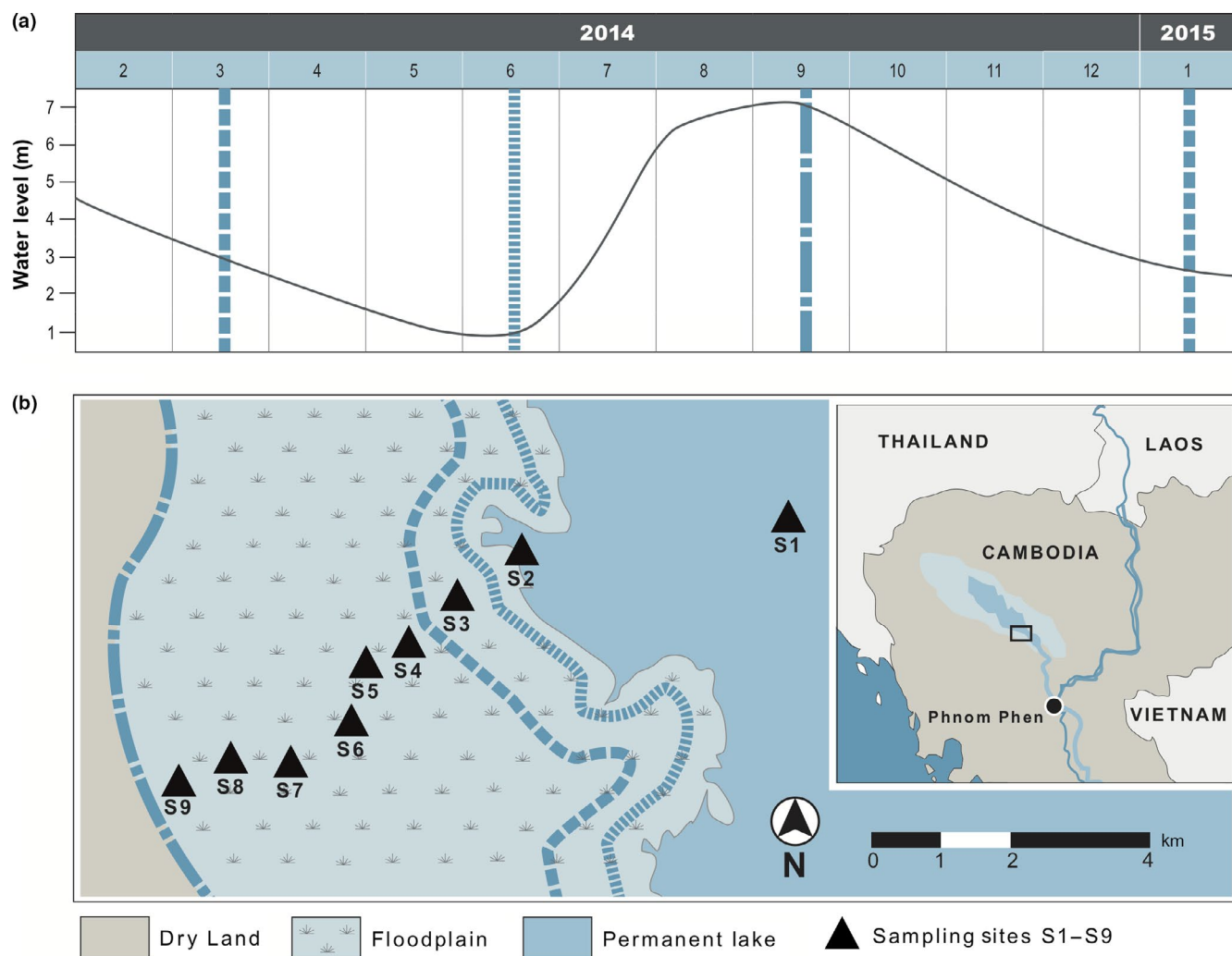
FIGURE 1 (a) Hydrograph for Tonle Sap Lake (TSL; Kampong Luong gauge station data); vertical hashed lines indicate each sampling event (March, June, September, and January). (b) Location of sampling sites ranging from the permanent lake (S1) to the lake fringe (S9). Hashed lines from the hydrograph data are overlaid to illustrate how water level varies throughout the seasons (Note: three sites were inundated during both the 2014 March and 2015 January sampling events, two sites during the 2014 June sampling event, and nine sites during the 2014 September sampling event). The inset map displays Cambodia (dark grey) and the TSL sampling location [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Statistical analyses

Ordination approaches were used to distinguish TSL species composition patterns across time and space. Of the 53 fish species collected during the study, six species were removed from our seasonal composition analysis because we collected fewer than five total specimens for those species across all seasons ($n = 47$, see Table S2 for species list). This step was taken because rare species are known to disproportionally influence ordination results, complicating their interpretation. First, correspondence analysis was used to assess seasonal variation in species composition across all four time periods. This approach maximizes the correspondence between species and sample scores (i.e. site scores) to increase the weighted correlation of scores in the first and subsequent axes. Compositional trends in the data were then analysed via ANOVA. Of course, the amount of flooded habitat available to fish tracks the flood cycle, so more sites were

included in the September sampling event (i.e. nine sites) than in June (i.e. two sites) or March/January (i.e. three sites). For this portion of the analysis, Poulsen et al. (2000) and regional experts were consulted to identify the a priori migratory status of each species (migratory versus resident) to determine if seasonal compositional patterns were influenced disproportionately by long-distance migratory species. Expert knowledge on species' migratory statuses was solicited from colleagues at University of Battambang, Ubon Ratchathani University, Kasetsart University, IFReDI, Mekong River Commission, and Texas A&M University. It should be noted that species actually engage in a wide spectrum of migratory distances within this region, but our coarse migratory designation may still assist with observing general patterns of temporal composition change within the assemblage.

Second, we used canonical correspondence analysis (CCA; ter Braak, 1986) to examine how environmental factors influence fish assemblage patterns spatially throughout the floodplain. The September

(a)

(b)
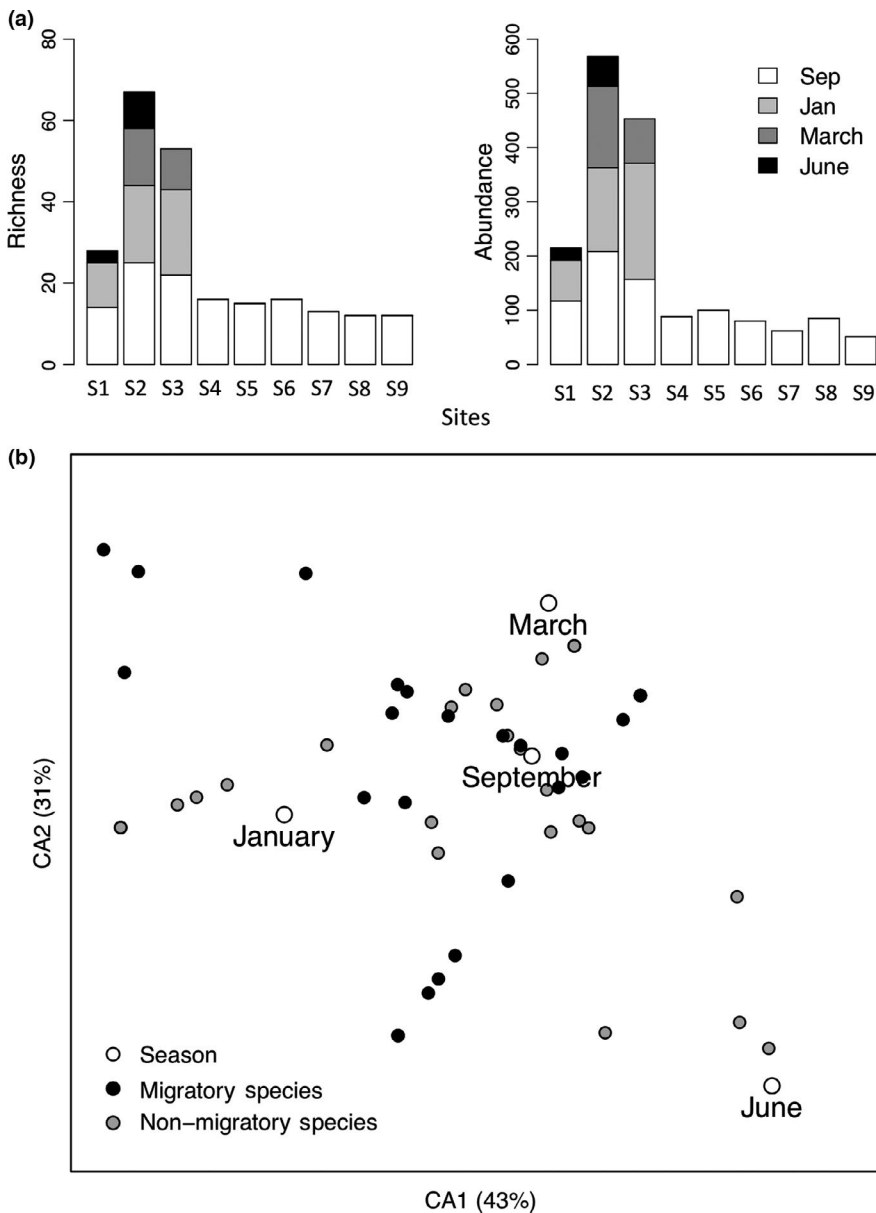
FIGURE 2 Fish assemblage (*n* = 47) richness and abundance across seasons (January, March, June, and September) in Tonle Sap Lake (TSL). (a) Summary of fish richness and abundances across the nine sites (S1–9) for each season. Note that the nets associated with S1 in March were not recovered. (b) Correspondence analysis (CA) ordination plot with solid points representing fish species and hollow points representing seasonal vector endpoints. See Figure 4 for species list with migratory status along with demersal and pelagic designations

data were exclusively used for this analysis (nine sites) because that sampling period captured the peak of water level inundation in the TSL, maximising both the number of mesohabitat sites represented and the total amount of fish captured. Species that had < 5 specimens collected during September were removed from this portion of our analysis, reducing our total species number down to 30 to explore wet season patterns across sites. We selected CCA because a detrended correspondence analysis indicated that, on average, the species (gradient level = 2.8) showed unimodal responses along the environmental gradients, making this constrained ordination approach the appropriate choice (Gauch, 1982; Palmer, 1993). A mantel test was then used to identify the significance of the environmental factors structuring the fish assemblage, and only those factors that were statistically significant ($p < 0.05$) were depicted on the ordination biplot. Environmental data were standardised using a mean-centred approach to prepare the data for use within our ordination methods. Species were also coded as

pelagic or demersal to see if this related to affinity for specific habitats in both the CCA analysis and species distributional abundances plot. In our study, demersal species were defined as fish that tend to stay in shallow water or primarily inhabit the bottom portion of the water column in deeper water. Pelagic species were defined as species that tend to use the entire water column or primarily inhabit the middle or surface waters. Fishbase (Froese & Pauly, 2017) was used to categorise fish species and regional experts were consulted to confirm the species designations as demersal or pelagic. Species were also coded as herbivore, omnivore, or piscivore to gain a better understanding of how trophic guild representation varied across mesohabitats during the wet season. Guild assignments were based on findings published by Pool et al. (2017) and McMeans et al. (2019) as well as unpublished stable isotope data for the Tonle Sap system. Lastly, site-level species abundances were plotted across the nine sites to explore species patterns from the exterior to the interior of the floodplain during the wet season.

FIGURE 3 Fish assemblage composition during the wet season (i.e. September). (a) Species water column association and trophic guide were identified across each mesohabitat site in the floodplain (S1–9). (b) Canonical correspondence analysis (CCA) ordination displaying the fish (species list in Figure 4), sites (black triangles) and the environmental characteristics (eigenvectors) selected from a forward stepwise selection of variables ($p < 0.05$)
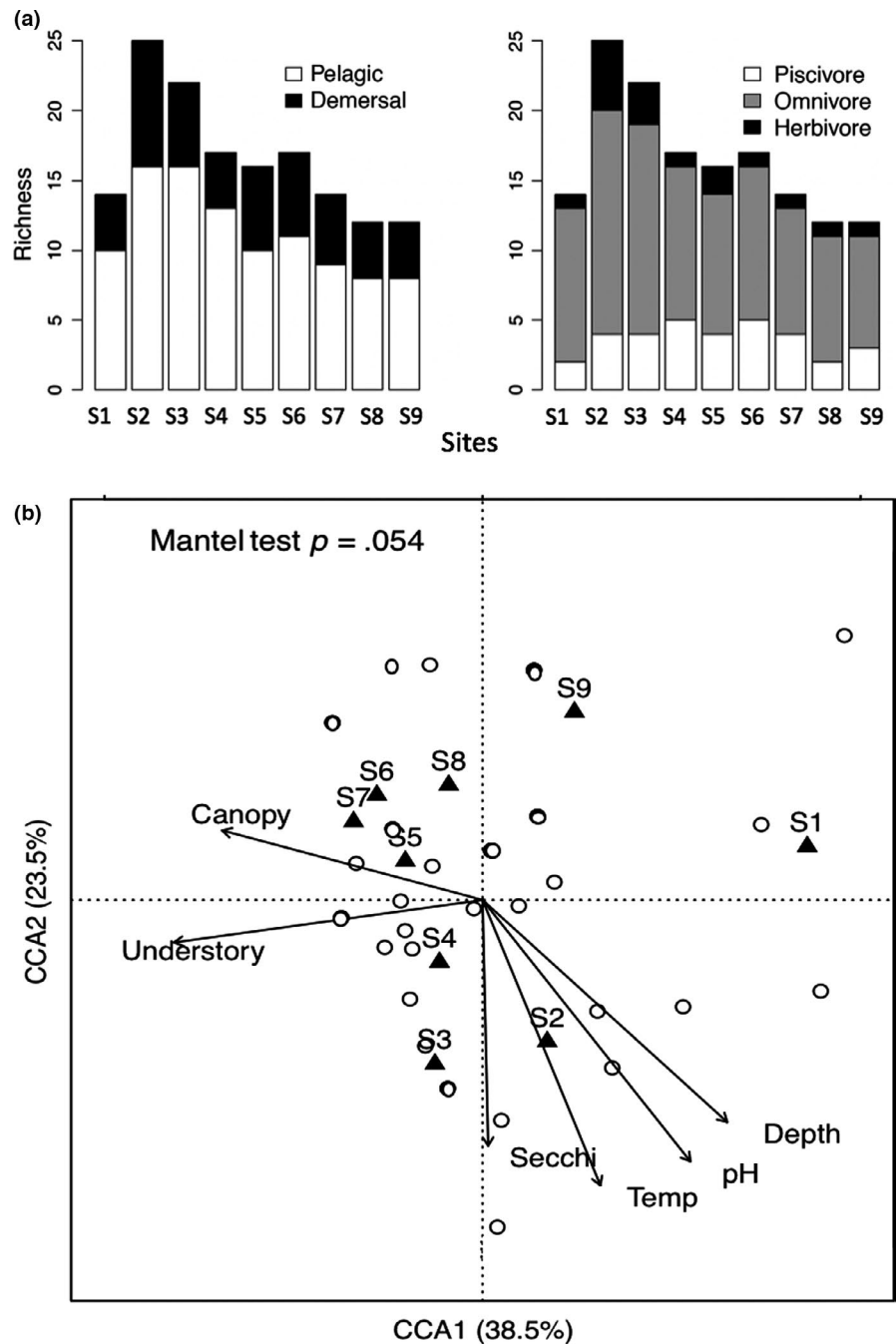
3 | RESULTS

3.1 | Seasonal fish assemblage composition

A total of 53 fish species and 1,584 individual fish specimens were collected across our 4 seasonal sampling events during the study. Significant differences in species richness were observed when comparing the number of species per site across seasons (ANOVA $p < 0.05$; Figure 2a,b), with the fewest total species identified in the low water month of June ($n = 9$) and the most species identified during the peak water month of September ($n = 43$) across all sites per season. Shifts in total catch abundance per site also occurred across seasons (ANOVA $p < 0.05$; Figure 2a,b), with the fewest total specimens

collected in June ($n = 81$) and the most specimens collected exclusively in September ($n = 869$) across all sites per season. For non-migratory species, specimens tended to be collected across multiple seasons with varying abundances across time, as evidenced by the common species *Rasbora aurotaenia*, *Paralaubuca typus*, and *Puntius brevis* (Figure 2b and Table S2). For migratory species, the highest abundances tended to be in September with more consistently reduced numbers during the dry season (Figure 2b and Table S2). The increased presence of common species such as *Henicorhynchus lobatus*, *Henicorhynchus siamensis*, and *Labiobarbus siamensis* during wet season is in-step with patterns observed in the downstream DIA fisheries that collect those species in high numbers during their migrations from the Tonle Sap to the Mekong River mainstem each year.

## 3.2 | Mesohabitat-level assemblage composition in the wet season

During the peak of the wet season (September), environmental factors associated with mesohabitat water chemistry and vegetation structure explained 62% of the variation in the fish assemblage within the first two canonical axes (Mantel test p = 0.054; Figure 3). Canopy coverage, understory coverage, water depth, secchi depth, surface pH, and surface temperature were identified as significant environmental variables influencing fish assemblage composition, corresponding with previous studies using similar approaches exploring how environmental variation structures tropical fish communities (Arthington, Balcombe, Wilson, Thoms, & Marshall, 2005; Rodriguez & Lewis, 1997). Open water and flooded forest edge (i.e. sites 1, 2, 3) exhibited higher depth, surface pH, temperature, and secchi depth compared to flooded middle forest and lake fringe sites (i.e. sites 4–8) that had increased canopy and understory cover (p < 0.05). Notably, despite DO failing to be identified as a significant factor structuring the whole fish assemblage in the floodplain, a substantial drop in DO was observed in sites 5–8 (lowest being 2.1 mg/L at site 7) in contrast to the deeper sites 1–4.

While most fish species displayed discontinuous distributions across floodplain sites, species richness and total abundance were highest at the edge of the flooded forest near the open water portion of the lake (i.e. S2–3; Figure 4). Pelagic species largely contributed to that pattern and tended to have their greatest abundances within flooded forest edge sites with lower abundances in other floodplain sites. Demersal species were found throughout the flooded forest edge, flooded middle forest, and lake fringe sites (Figure 4). Only the

pelagic species *Paralaubuca typus* was collected at every site (i.e. S1–9; Figure 4). There was also no clear pattern associated with species' size across sites during the wet season (Figure 5). For example, while specimens of *L. siamensis* ranged considerably in size (70–208 mm), small and large individuals were observed across sites ranging from the interior to the exterior of the floodplain.

4 | DISCUSSION

We found the association between the TSL fish assemblage and the floodplain mesohabitats to be structured both temporally and spatially. Seasonal changes in the fish assemblage composition were driven principally by an increase in the occurrence and abundance of migratory species during the wet season. The assemblage was further structured spatially by environmental factors during the wet season, suggesting that the physical and chemical floodplain template substantively influences mesohabitat-scale fish composition during high water periods. However, most species were not limited exclusively to one or two mesohabitats during peak inundation, indicating that species tend to use a composite of mesohabitats during seasonal flooding events. When considered cumulatively, mesohabitat use by fishes within the TSL was environmentally structured and seasonally dynamic, suggesting that a variety of species' life-history characteristics shape compositional patterns within the floodplain environment. These findings also illustrate the importance of the natural flow regime for maintaining the lake's diverse fish composition and the need for preserving multiple mesohabitat types within tropical floodplains.
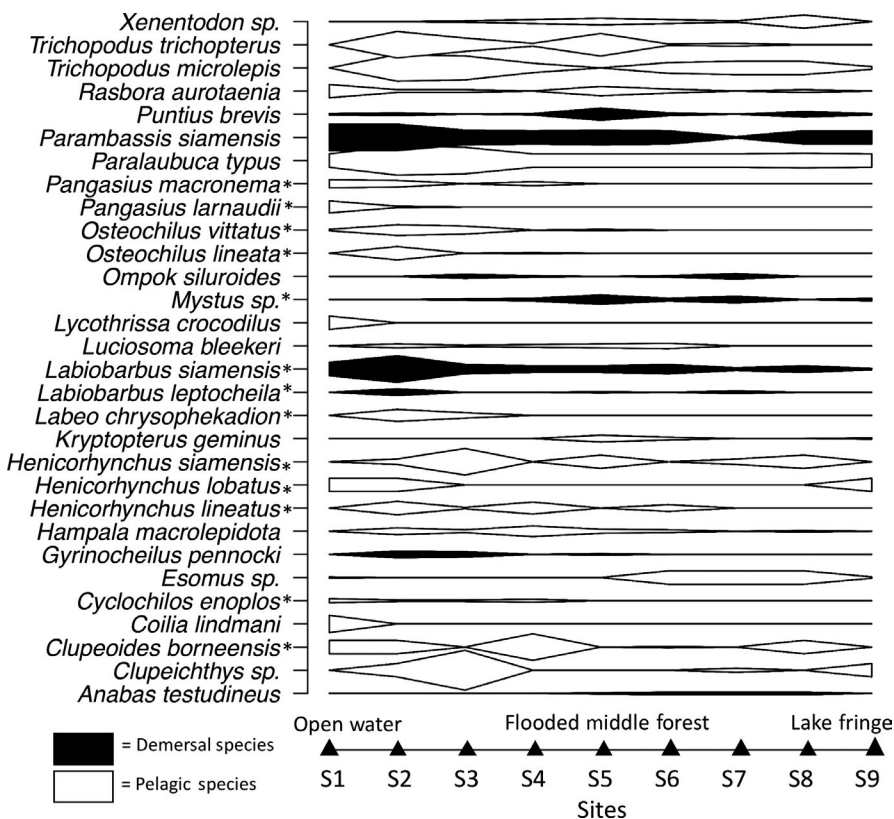
FIGURE 4 Distribution of the most abundant fish species across the nine sites during the wet season. Species (n = 30) were included here if > 10 specimens were collected cumulatively across all nine sites. The greatest species width displayed above represents an abundance of 34 individuals (see *Clupeichthys* sp. at S3). Each species' predicted position in the water column (demersal or pelagic) is indicated by the polygon colour and migratory species are indicated with a star symbol (*). Species photos and language translations can be found in Kano et al. (2013)
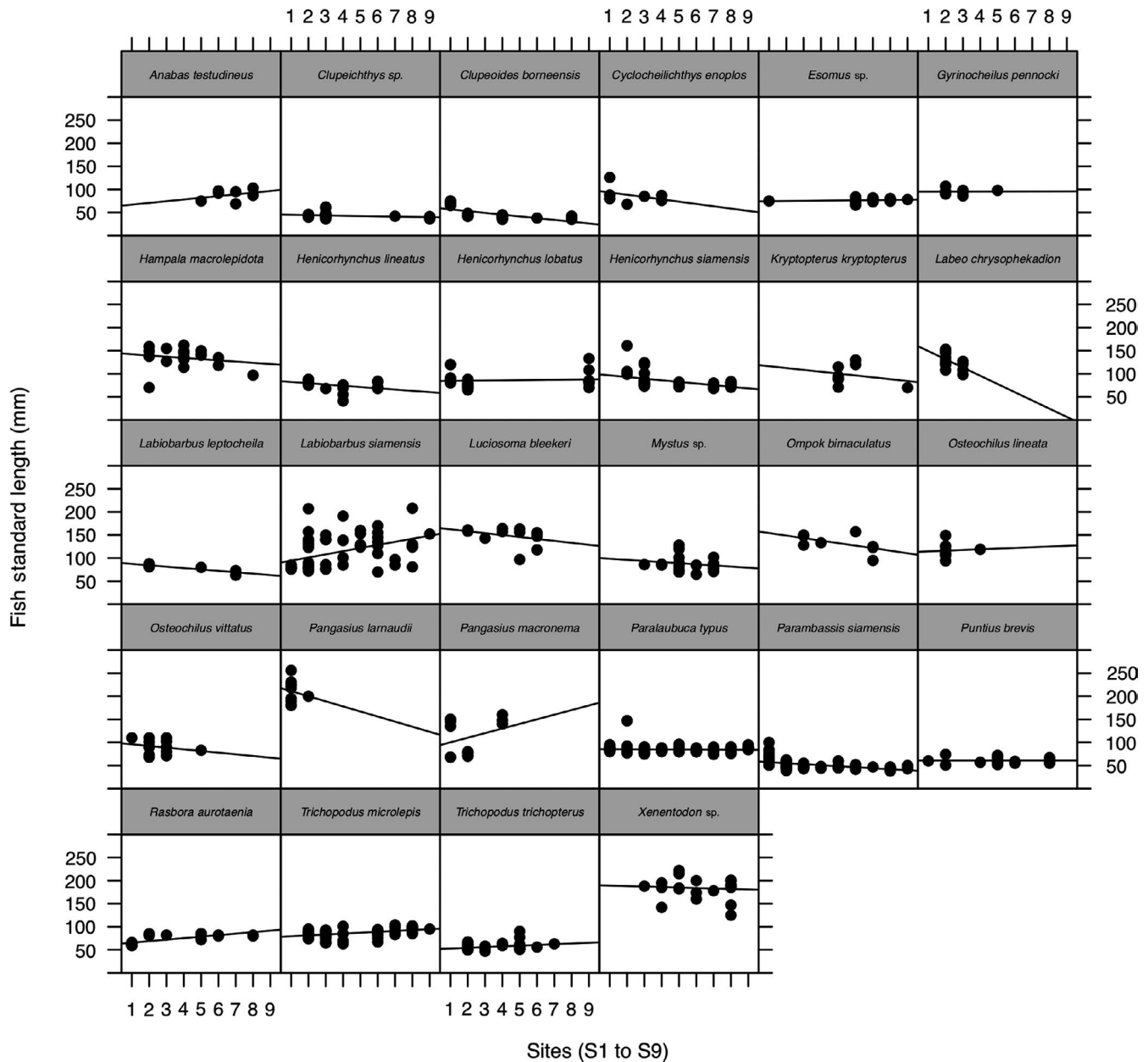
FIGURE 5 Relationship between fish standard length and their wet season catch site within the floodplain were used for simple linear regression. Please note that *Coilia lindmani* was not included above because specimens for that species were only found in one site (S1) during the September sampling event

Seasonal changes in the fish assemblage were observed, with greater species richness and abundances occurring during the wet season. As predicted, the compositional shift was associated with dissimilarities in fishes' life-history characteristics across seasons (i.e. the increased occurrence of migratory species at the peak of floodplain inundation). Fish migration within flood–pulse systems is common, but the total distance that particular species travel can vary considerably, impacting the seasonal composition patterns of local assemblages. In TSL, several species are believed to undergo short-distance movements from the pelagic open lake into the floodplain during the wet season, whereas others participate in long-distance migrations to the mainstem Mekong River (Poulsen et al.,

2000). For example, species such as *Cyclocheilichthys enoplos* that are known to migrate for breeding purposes between flooded forest habitat and the Mekong mainstem were abundant in the TSL floodplain during the wet season and were completely absent during the dry season. In contrast, the resident *Anabas testudineus* was found year-round, primarily moving from the edge of the flooded forest during the dry season to the floodplain interior during the wet season. Given that our sampling focused predominantly on the floodplain with minimal permanent lake sampling throughout the year, we regrettably cannot determine whether the seasonal floodplain composition shifts we observed were driven primarily by small- or large-scale fish migrations, yet both are likely to be important for

understanding seasonal assemblage changes. As such, a shifting cast of species must be integrated into food web trophic structure (Pool et al., 2017) and stability analyses to realistically model flood–pulse assemblage dynamics across seasons.

Deconstructing how mesohabitat heterogeneity influences fish assemblage composition patterns is inherently challenging because flood–pulse systems tend to have environmental characteristics that fluctuate drastically in response to seasonally changing water levels. Some studies have also found that principal physical, chemical, and biological aspects of floodplain habitats can become homogenised during peak periods of flood inundation (Thomaz, Bini, & Bozelli, 2007). Nevertheless, we found that environmental variables structured the mesohabitat-level fish composition during the wet season. More specifically, vegetative structure and water habitat characteristics defined the fish assemblage with factors such as high understory density, canopy density, pH, water clarity, and total depth tending to have a positive association with elevated species richness and abundance levels. Similarly, Arrington and Winemiller (2006) found that fish assemblage composition in the floodplain of the Cinaruco River (Venezuela) was significantly influenced by mesohabitat parameters such as water depth, sampling period, and location of the site in the landscape. However, some TSL species displayed unique mesohabitat associations that contrasted with the pattern displayed by the assemblage as a whole. For instance, the demersal *Anabas testudineus* occurred exclusively within the warm, oxygen-poor shallow waters of the floodplain during the wet season. Physiological tolerances appear to considerably influence this species' individual mesohabitat-scale associations, despite most species maintaining occupancy across more oxygen-rich sites throughout the floodplain. In-step with our prediction, our study found that the fish assemblage displayed environmentally mediated spatial structure but it remains unknown to what extent deterministic interactions (i.e. predation and competition) further sway species use of specific mesohabitats within floodplain systems.

In contrast to our rudimentary prediction that trophic guild and benthic–pelagic differences would influence deep to shallow floodplain mesohabitat associations, we identified comparable representation of species with unique trait characteristics across our depth gradient (i.e. pelagic predators did not universally associate with deep mesohabitats nor did benthic omnivores and herbivores universally associate with shallow mesohabitats). In concurrence with our findings, recent telemetry work on floodplain predators such as the *Lepisosteus platyrhinchus* (i.e. Florida Gar) in the Florida Everglades (U.S.A.) has shown that high trophic-level species can display very flexible habitat associations that accommodate the influence of landscape context on hydrology and distance to drought refuges. Current research studying omnivore foraging in the TSL has also shown that several fish species shift to more invertebrate-dominated diets during the wet season (McMeans et al., 2019), ostensibly to utilise the entire floodplain network of mesohabitats that host abundant benthic invertebrate communities. Interestingly, we found that the flooded forest edge directly adjacent to the permanent lake's open water was the most species-rich and tended to have the highest abundances for all trophic guilds

during the wet season. We suspect that the flooded forest edge provides vegetative structure for predator avoidance while also providing optimal foraging access to both open water and floodplain environments. For instance, the planktivorous and pelagic *P. typus* was found in every site during the wet season but its greatest abundances were in the flooded forest edge sites. Adding further complexity at the assemblage level and in contrast to the overall pattern of increased species richness and abundance in the flooded gallery forest edge sites, some species (benthic and pelagic) were found in greater abundances at the *leading edge* of the flooded forest water line in response to seasonal flooding. Consequently, it is clear that multiple life-history traits are influencing complex species-specific mesohabitat associations within the TSL floodplain.

An unexpected finding associated with our wet season species distribution results included a lack of size-related variation in intraspecies occupancy across floodplain mesohabitats. Typically, within aquatic systems, larger individuals of a given species tend to occupy deep water habitats while smaller individuals tend to occupy shallow water habitats (Copp, 1997; Santos, Godinho, & Ferreira, 2004). Predation by gape-limited piscivores is the principal mechanism hypothesised to reinforce those shifts in species' depth distributions associated with their size-class (Morán-López, Pérez-Bote, da Silva, & Casildo, 2012). In contrast, for the size ranges that we collected, intraspecies size-dependent variation was not consistently displayed from deep to shallow mesohabitats. For example, we collected the full range of *L. siamensis* size-classes at most of our mesohabitat sites. We speculate that the generally dense submerged vegetation and high suspended sediment loads within the floodplain during the wet season may minimise the disparity in predation risk between deep and shallow TSL mesohabitats. The wealth of resources available during the wet season throughout the floodplain (i.e. plankton, periphyton, invertebrates, forage fish) for fishes from all different trophic guilds may also be incentivising small and large fish alike to forage across multiple mesohabitats, irrespective of water depth. Future work will focus on this thread of exploration to clearly discern how species size-class and mesohabitat variables influence intraspecies distribution patterns within the TSL floodplain.

Reduced habitat complexity within freshwater systems around the world has negatively impacted fish communities (Smokorowski & Pratt, 2007). Specifically, within flood–pulse systems, our findings illustrate that mesohabitat heterogeneity may be an essential component supporting fish assemblage diversity. These results are conservation-relevant because over 200 dams are in development or scheduled for construction in the Mekong River Basin (MRC 2009). They are expected to profoundly alter the TSL hydrology, which, in turn, will alter the amount and duration of flooding within the systems' floodplain (Arias, Cochrane, Kummub, et al., 2014). Those flow regime changes will reduce the availability of some habitat types to the TSL's diverse array of fish species. Logging and agricultural development are further homogenising floodplain habitats along most of the perimeter of the lake (Arias, Cochrane, & Elliott, 2014; MRC, 2009). An additional conservation concern is that migratory species abundant in the economically important stationary trawl (Dai) fishery (e.g. *Henicorhynchus*

and *Labiobarbus* sp.) occur in both the interior and exterior of the TSL floodplain during the wet season. Taken together, these ecologically and economically important migratory Dai fishery species may experience cumulative negative impacts within the Lower Mekong Basin in the coming years, adversely impacting their ability to persist in high abundances or resiliently respond to future pressures such as overharvest and climate change.

A limitation of this study was the narrow spatial scope that was captured within our sampling design. The floodplain of the TSL is a difficult environment to study, making it challenging to conclude how floodplain characteristics in less accessible parts of the lake might differentially influence local fish composition patterns. Furthermore, while we collected the most abundant species known to occur within the lake, the 53 species in our study represent only a portion of the *c.* 150 species that are believed to occur in the TSL (Campbell, Poole, Giesen, & Valbo-Jorgensen, 2006; MRC, 2009). Fishermen in the lake use over 200 different gear types including gill nets, basket traps, trawl, and seine nets, strategically placing their gear in habitats dependent on the water levels (Deap, Degen, & van Zalinge, 2003). This type of comprehensive fishing capacity was not replicated in our study. Nevertheless, we assert that the species collected in our study illustrate how the floodplain community is structured.

In conclusion, given that almost all species occurred in multiple floodplain mesohabitats during the wet season, habitat heterogeneity and accessibility appear to be fundamental for maintaining the high species diversity that characterises the TSL. Together, land conversion, reduced nutrient transport, and flow regime change can be expected to significantly alter fishes' use of the floodplain habitat mosaic, potentially eroding the system's ecological stability, while also negatively impacting the human systems that depend upon it. More broadly, our findings suggest that future habitat homogenization may negatively impact a wide range of taxonomically and functionally diverse fish species within flood–pulse environments around the world. Reduced habitat complexity within systems such as the Indus, Yangtze, and Amazon Rivers may not simply impact a few fish species with specific traits (i.e. benthic forage fish or pelagic predators). Instead, habitat simplification may modify entire aquatic food webs that are dependent on species' seasonal access to multiple floodplain habitat types. Therefore, to effectively protect fish communities within flood–pulse systems, conservation efforts must be made to minimize mesohabitat-scale land conversion for agricultural and timber harvest purposes. Simultaneous efforts to maintain natural flow regime patterns and mitigate the impacts of regional hydropower development are also needed to promote fish access to those complex floodplain environments.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Thomas Pool 🄳 https://orcid.org/0000-0001-6920-4050
Chuanbo Guo 🄳 https://orcid.org/0000-0002-9807-3915

REFERENCES

Arias, M. E., Cochrane, T. A., & Elliott, V. (2014). Modelling future changes of habitat and fauna in the Tonle Sap wetland of the Mekong. *Environmental Conservation, 41*, 165–175.

Arias, M. E., Cochrane, T. A., Kummub, M., Lauric, H., Holtgrieve, G., Koponenc, J., & Piman, T. (2014). Impacts of hydropower and climate change on drivers of ecological productivity of Southeast Asia's most important wetland. *Ecological Modelling, 272*, 252–263.

Arias, M. E., Cochrane, T. A., Norton, D., Killeen, T. J., & Khon, P. (2013). The flood pulse as the underlying driver of vegetation in the largest wetland and fishery of the Mekong Basin. *Ambio, 42*, 864–876.

Arias, M. E., Cochrane, T. A., Piman, T., Kummu, M., Caruso, B. S., & Killeen, T. J. (2012). Quantifying changes in flooding and habitats in the Tonle Sap Lake (Cambodia) caused by water infrastructure development and climate change in the Mekong Basin. *Journal of Environmental Management, 112*, 53–66.

Arias, M. E., Wittmann, F., Parolin, P., Murray-Hudson, M., & Cochrane, T. A. (2018). Interactions between flooding and upland disturbance drives species diversity in large river floodplains. *Hydrobiologia, 814*, 5–17.

Arrington, D. A., & Winemiller, K. O. (2006). Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. *Journal of the North American Benthological Society, 25*, 126–141.

Arthington, A. H., Balcombe, S. R., Wilson, G. A., Thoms, M. C., & Marshall, J. (2005). Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. *Marine and Freshwater Research, 56*, 25–35.

Bonheur, N., & Lane, B. D. (2002). Natural resources management for human security in Cambodia's Tonle Sap Biosphere Reserve. *Environmental Science & Policy, 5*, 33e41.

Campbell, I. C., Poole, C., Giesen, W., & Valbo-Jorgensen, J. (2006). Species diversity and ecology of Tonle Sap Great Lake, Cambodia. *Aquatic Sciences, 68*, 355–373.

Carpenter, S. R., & Kitchell, J. F. (1993). *The trophic cascade in lakes*. Cambridge, UK: Cambridge University Press.

Castello, L. (2008). Lateral migration of *Arapaima gigas* in floodplains of the Amazon. *Ecology of Freshwater Fish, 17*, 38–46.

Copp, G. H. (1997). Microhabitat use of fish larvae and 0+ juveniles in a highly regulated section of the river Great Ouse. *Regulated Rivers: Research & Management, 13*, 267–276.

Costa-Cabral, M. C., Richey, J. E., Goteti, G., Lettenmaier, D. P., Feldkotter, C., & Snidvongs, A. (2008). Landscape structure and use, climate, and

water movement in the Mekong River basin. *Hydrological Processes*, *2274*, 2267–2274.

Deap, L., Degen, P., & van Zalinge, N. (2003). Fishing Gears of the Combodian Mekong. Phnom Penh, Cambodia.

Fernandes, C. C. (1997). Lateral migration of fishes in Amazon floodplains. *Ecology of Freshwater Fish*, *6*, 36–44.

Foti, R., del Jesus, M., Rinaldo, A., & Rodriguez-Iturbe, I. (2012). Hydroperiod regime controls the organization of plant species in wetlands. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 19596–19600.

Froese, R., & Pauly, D. (2017). FishBase. Retrieved from www.fishbase.org

Gauch, H. G. (1982). *Multivariate analysis in community ecology*. Cambridge, UK: Cambridge University Press.

Godinho, A. L., Lamas, I. R., & Godinho, H. P. (2010). Reproductive ecology of Brazilian freshwater fishes. *Environmental Biology of Fishes*, *87*, 143–162.

Goulding, M. (1980). *The fishes and the forest*. Berkeley, CA: University of California Press.

Holtgrieve, G. W., Arias, M. E., Irvine, K. N., Lamberts, D., Ward, E. J., Kummu, M., … Richey, J. E. (2013). Patterns of ecosystem metabolism in the Tonle Sap Lake, Cambodia with links to capture fisheries. *PLoS ONE*, *8*, e71395.

Hortle, K. G. (2007). Consumption and the yield of fish and other aquatic animals from the Lower Mekong Basin. *MRC Technical Paper No. 16*, 87.

Jardine, T. D., Bond, N. R., Burford, M., Kennard, M. J., Ward, D. P., Bayliss, P., … Bunn, S. E. (2015). Does flood rhythm drive ecosystem responses in tropical riverscapes? *Ecology*, *96*, 684–692.

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, *106*, 110–127.

Kano, Y., Adnan, M. S., Grudpan, C., Grudpan, J., Magtoon, W., Musikasinthorn, P., … Yamashita, P. (2013). An online database on freshwater fish diversity and distribution in Mainland Southeast Asia. *Ichthyological Research*, *60*, 293–295.

Keskinen, M., Kummu, M., Salmivaara, A., Someth, P., Lauri, H., de, Moel, H., … Pech, S. (2013). Tonle Sap now and in the future? Final Report of the Exploring Tonle Sap Futures study. Espoo: Water & Development Publications.

McMeans, B. C., Kadoya, T., Pool, T. K., Holtgrieve, G. W., Lek, S., Kong, H., … McCann, K. S. (2019). Consumer trophic positions respond variably to seasonally fluctuating environments. *Ecology*, *100*, e02570.

Morán-López, R., Pérez-Bote, J. L., da Silva, E., & Casildo, A. B. P. (2012). Hierarchical large-scale to local-scale influence of abiotic factors in summer-fragmented Mediterranean rivers: Structuring effects on fish distributions, assemblage composition and species richness. *Hydrobiologia*, *696*, 137–158.

MRC (2009). Mekong River Commission Spatial Database.

Palmer, M. W. (1993). Putting things in even better order: The advantages of canonical correspondence analysis stable. *Ecology*, *74*, 2215–2230.

Parolin, A. P., De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., … Junk, W. J. (2004). Central Amazonian floodplain forests: Tree adaptations in a pulsing system Published by : Springer on behalf of New York Botanical Garden Press Stable URL : http://www.jstor.org/stable/4354485. *The Botanical Review*, *70*, 357–380.

Pool, T., Holtgrieve, G., Elliott, V., McCann, K., McMeans, B., Rooney, N., … Chhuoy, S. (2017). Seasonal increases in fish trophic niche plasticity within a flood-pulse river ecosystem (Tonle Sap Lake, Cambodia). *Ecosphere*, *8*, e01881.

Poulsen, A. F., Valbo-Jørgensen, J., Chan, S., Chhuon, K. C., Viravong, S., Bouakhamvongsa, K., … Tran, Q. B. (2000). Fish Migrations and spawning habits in the Mekong mainstream – A survey using local knowledge (basin-wide). Assessment of Mekong Fisheries: Fish Migrations and Spawning and the Impact of Water Management Component, Vientiane.

Robinson, C. T., Tockner, K., & Ward, J. V. (2002). The fauna of dynamic riverine landscapes. *Freshwater Biology*, *47*, 661–677.

Rodriguez, M., & Lewis, W. M. (1997). Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs*, *67*, 109–128.

Röpke, C. P., Ferreira, E., & Zuanon, J. (2014). Seasonal changes in the use of feeding resources by fish in stands of aquatic macrophytes in an Amazonian floodplain, Brazil. *Environmental Biology of Fishes*, *97*, 401–414.

Santos, J. M., Godinho, F. N., & Ferreira, M. T. (2004). Microhabitat use by Iberian nase *Chondrostoma polylepis* and Iberian chub *Squalius carolitertii* in three small streams, north-west Portugal. *Ecology of Freshwater Fish*, *13*, 223–230.

Schindler, D. E., Carpenter, S. R., Cole, J. J., Kitchell, J. F., & Pace, M. L. (1997). Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science*, *277*, 248–251.

Schindler, D. E., & Scheuerell, M. D. (2002). Habitat coupling in lake ecosystems. *Oikos*, *98*, 177–189.

Smokorowski, K. E., & Pratt, T. C. (2007). Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems – A review and meta-analysis. *Environmental Reviews*, *41*, 15–41.

ter Braak, C. (1986). Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology*, *67*, 1167–1179.

Thomaz, S. M., Bini, L. M., & Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, *579*, 1–13.

Valle Ferreira, L., & Stohlgren, T. J. (1999). Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia*, *120*, 582–587.

Vanni, M. J. (2002). Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, *33*, 341–370.

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*, 130–137.

Wantzen, K. M., Junk, W. J., & Rothhaupt, K. O. (2008). An extension of the floodpulse concept (FPC) for lakes. *Hydrobiologia*, *613*, 151–170.

Wilkes, M. A., Maddock, I., Link, O., & Habit, E. (2016). A community-level, mesoscale analysis of fish assemblage structure in shoreline habitats of a large river using multivariate regression trees. *River Research and Applications*, *32*, 652–665.

Wood, B. M., & Bain, M. B. (1995). Morphology and microhabitat use in stream fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*, 1487–1498.

Worbes, M. (1985). Structural and other adaptations to long-term flooding by trees in central Amazonia. *Amazoniana*, *9*, 459–484.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.