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Fish assemblages of an African river floodplain: a test of alternative models of community structure

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Abstract – In the Oueme River, a lowland river in Benin, Africa, artificial ponds constructed in the floodplain (whedos) are colonised during the high-water period by a presumably random sample of fishes from the river channel. As water slowly recedes from the floodplain, fishes are isolated in whedos until they are harvested near the end of the dry season. We surveyed fishes in whedos and adjacent main-channel and floodplain habitats during two low-water periods (2008 and 2009) and one falling-water period (2010–2011) to evaluate the relevance of four alternative metacommunity models to these systems. In 2010–2011, we also measured a suite of physicochemical variables including dissolved oxygen, temperature, specific conductivity and per cent cover of aquatic vegetation. Whedos were covered with dense growth of aquatic vegetation, and dissolved oxygen concentrations were lower in whedos and a natural floodplain depression compared with the main channel. Multivariate analyses revealed that habitat types were distinct with regard to assemblage structure and abiotic conditions. Assemblages in whedos and natural floodplain depressions were differentiated from those of the river channel, with the floodplain habitats being dominated by piscivorous fishes that tolerate aquatic hypoxia. Dispersal, aquatic hypoxia and predation act in concert to shape local community structure. Patch dynamics, species sorting and mass effect models all were consistent with patterns in fish assemblage structure in this system. We conclude that the underlying mechanisms of drift, speciation, selection and dispersal ultimately may be more useful for explaining patterns in ecological communities than alternative metacommunity models.

Key words: Benin; fish assemblage structure; floodplain; environmental filtering; aerial respiration; metacommunity

Introduction

Early models of community structure and dynamics mainly focused on species interactions such as competition and predation that limit population growth. More recent metacommunity models add to this a consideration of how spatiotemporal environmental variation and movement affect community dynamics (Leibold et al. 2004; Holyoak et al. 2005). Following Leibold et al. (2004), we define *metacommunity* as a set of local communities that are linked by dispersal of multiple potentially interacting species. The *patch dynamics* model hypothesises that local community composition derives from a trade-off between competitive ability and dispersal ability (Hutchinson 1953; Townsend 1989). Environmental disturbance provides opportunity for competitively inferior species to colonise habitat patches and persist until they are displaced by competitively superior species or impacted by a subsequent disturbance. Even if disturbance and colonisation dynamics are essentially stochastic, the model assumes nonrandom sequences of local community transition resulting from differential colonisation and competitive abilities. In contrast, the *species sorting* model predicts that community structure is a result of environmental heterogeneity and the habitat selection and environmental filtering that result from it (Whittaker 1962; Holt 1985). The *mass*

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effect model proposes that community structure is a function of spatial dynamics whereby dispersal following source–sink population dynamics allows for competitively inferior species to persist in local patches by immigration of individuals from patches where abiotic and biotic conditions are more favourable (Shmida & Wilson 1985; Pulliam 1988; Leibold et al. 2004). Finally, the *neutral* model of metacommunity dynamics (Hubbell 2001) provides a sort of null model to which predictions from other models can be compared. According to the neutral model, species are equivalent in their dispersal and competitive abilities so that community structure largely results from stochastic processes. In a recent conceptual synthesis of community ecology, Vellend (2010) proposed that community structure is a product of selection, drift, speciation and dispersal, with some of these processes assuming greater importance at certain times and places.

Since their advent, these alternative metacommunity models have been used to explain fish community structure in lotic and floodplain habitats. For example, several studies have invoked the species sorting concept to explain fish community structure (e.g., oxbow lakes, Winemiller et al. 2000; floodplain river, Arrington & Winemiller 2006; stream, Hoeinghaus et al. 2007). In a study of ephemeral freshwater pond communities, Urban (2004) advocated the necessity of integrating the species sorting and mass effect models if metacommunity theories are to be successfully applied. The patch dynamics model frequently has been used to explain community structure in streams and rivers (Pringle et al. 1988; Townsend 1989; Winemiller et al. 2010). Walker & Cyr (2007) used the neutral model to describe fish and zooplankton communities of lakes worldwide, but the model was unable to predict phytoplankton community structure.

In the Oueme River, a lowland river in Benin, West Africa, artificial ponds constructed in the floodplain (whedos) enhance floodplain fisheries of rural communities, and also provide an opportunity to evaluate how well alternative metacommunity models predict species assemblage structure in a seasonally dynamic system. This study investigated fish assemblages in floodplain habitats of the Oueme River at the beginning of the dry season when they first become isolated, and at the end of the dry season when they are harvested. Of particular interest was the question of whether species assemblages in floodplain habitats result from stochastic colonisation during annual floods (the null model), or whether they are strongly influenced by biotic interactions and/or environmental filtering. When the Oueme River breaches its banks during the annual flood pulse, fishes disperse into productive floodplain habitats with good water quality to exploit abundant resources and to spawn. As water levels gradually fall, many fishes disperse back to the river channel, but juveniles in particular can remain in structurally complex aquatic habitats of the floodplain where current velocity is lower (Winemiller 1996). At the same time, increasingly dense growth of floating aquatic macrophytes causes dissolved oxygen in whedos to decline. We anticipated that whedos would become dominated by fish species that possess adaptations for aerial respiration (Junk et al. 1989; Winemiller 1996). Predatory fishes having adaptations for aerial respiration, such as walking catfishes (*Clarias agboyiensis*, *C. gariepinus)*, the bichir *Polypterus senegalus,* the snakehead *Parachanna obscura* and the lungfish *Protopterus annectens*, are common in lowland rivers of West Africa. At the end of the dry season, whedo fish assemblages may be influenced by competition within the top trophic level in addition to predation and environmental filtering in response to hypoxia. Thus, we also anticipated that as the dry season progresses and young fishes grow and coexist in whedos at ever increasing densities, species richness would decline.

We expected that fish assemblage dynamics in whedos would be consistent with the patch dynamics model whereby less-competitive or vulnerable species are initially common during the flood pulse, and are then largely replaced by superior competitors and predators during the period of patch isolation. The species sorting model also may apply to this system, because aquatic hypoxia during whedo isolation favours tolerant fish species. We expected that the mass effect model would not describe this system, because once whedos become isolated, there essentially is no dispersal and interannual survival of resident fishes is low because fishermen remove nearly all fishes at the end of the dry season. Thus, we did not expect fishes to reflect random assemblage structure at the end of the dry season.

Methods

Study site

The Oueme River flows from its headwaters in the Atacora Mountains in Benin (West Africa) approximately 500 km to Lake Nokoue, a large brackish estuary that empties into the Gulf of Guinea near the city of Cotonou. The Oueme's average discharge is 170 m^3/s. The Oueme Basin supports approximately 116 fish species (Lévêque et al. 1990, 1992). The study area was located near the town of Adjohoun in the south-central region of Benin (Fig. 1). The region experiences a major wet season from March to July

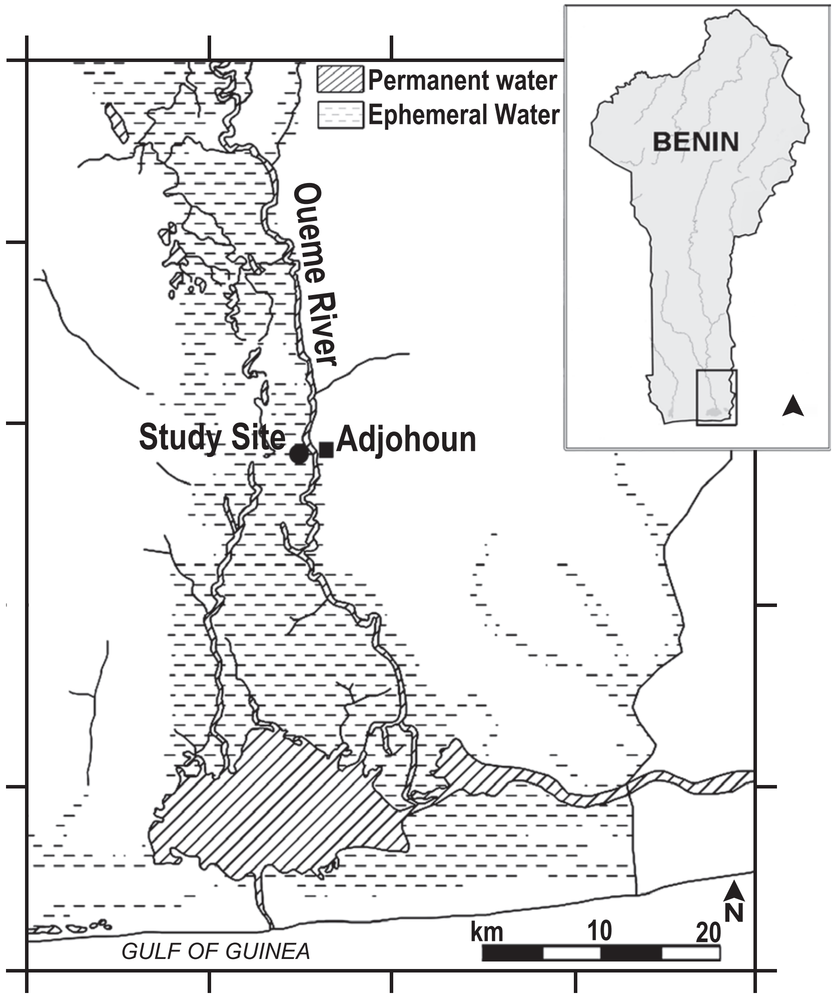

Fig. 1. Map of study location in the Oueme River Basin, Benin, West Africa.

and a minor wet season from September to mid-November, with other months receiving little or no rainfall (Adite et al. 2005). On the floodplain near Adjohoun, the dominant land uses are small-scale farming and aquaculture in ponds called whedos. Whedos are long, narrow ponds constructed in the floodplain that hold fishes that colonise from the river during the annual flood pulse (Welcomme et al. 2006; Hauber et al. 2011a,b). Whedos in the study area are, on average, 1 m deep by 5.5 m wide and range from 40 to 1000 m in length. During the dry season, whedos are unmanaged and become covered with aquatic macrophytes that create conditions of low dissolved oxygen (DO) as a result of tissue senescence, decomposition, microbial respiration and inhibition of gas exchange at the water surface. Whedos are harvested at the end of the dry season by first isolating a section of the whedo with nets, then removing all of the aquatic vegetation in that section. Fishes are then harvested by hand in the cleared section before the barrier net is used to encircle the remaining fish and vegetation in a purse seine fashion. This process is then repeated sequentially in sections along the entire length of the whedo.

Akadjavi (akadja of small size) is another form of aquaculture practised in the region. Akadjavis are built along the bank of the Oueme River at the onset of the dry season after the floodwaters have receded. Terrestrial vegetation is arranged in rectangular plots that are surrounded and held in place with sticks or palm fronds lodged in the sediment. Akadjavis are constructed to attract fishes and provide structurally complex habitat and hard substrate for benthic microorganisms. After several weeks to a month or more, each akadjavi is encircled with a net, vegetation is removed from within and entrapped fishes are harvested by pulling the net onto land in a purse seine manner.

Sample collections – low-water periods

Fishes were surveyed in nine whedos, one natural floodplain depression and one site in the Oueme River from May to July (late dry season) 2008, and in 11 whedos, one natural floodplain depression and one site in the Oueme River from February to March 2009 (low-water period). First, a 20 m reach at one end of the whedo was blocked with a 2 cm mesh barrier net, aquatic vegetation was removed and the area was seined (2 × 6 m seine with 0.5 cm mesh) five times before encircling the area with the barrier net to capture any remaining fishes. A 2 × 6 m seine with 0.5 cm mesh was used to survey natural depressions in the floodplain. To survey fishes from structurally complex habitat along the shoreline of the river channel, we collected akadjavis. The area was encircled with a net (2 cm mesh), all sticks and vegetation were checked for fishes before being removed, and the net was pulled from the water to capture the remaining fish. A 2 m cast net (1 cm mesh) also was used to sample adjacent open-water areas in the main channel. Captured fishes were euthanised using tricaine methanesulphonate (MS-222) following Texas A&M Animal Use Protocol 2005–117, and then preserved in formalin. Specimens were identified using taxonomic keys in Lévêque et al. (1990, 1992). Voucher specimens were catalogued into the Texas Cooperative Wildlife Collection at Texas A&M University.

Sample collections–falling-water period

To compare fish assemblage structure of floodplain habitats between the low-water and falling-water hydroperiods, fishes were again surveyed from 11 whedos plus one natural floodplain depression and one site in the Oueme River channel during the falling-water period of December 2010 and January 2011. To allow for estimates of abundance in terms of catch-per-unit effort (CPUE), dimensions of each sampled habitat were measured, including the transect length, transect width and thalweg depth. The area and water depth of the akadjavi was measured. For the river channel, CPUE was calculated based on the volume of the akadjavi and also based on the total volume sampled by the cast net (diameter x depth summed for all throws). Wet weights of captured fishes were recorded for later estimation of total fish biomass per unit volume.

Physicochemical variables–falling-water period

Physicochemical variables were not measured at the survey sites during low-water periods in 2008 and 2009 because equipment was not available. DO (mg/L), conductivity (μS/cm), pH and temperature (ºC) were measured during December 2010 and January 2011 in each habitat with a Hach minisonde. Measurements were taken every 10 minutes for approximately 2 hours. Replicate conductivity, pH and temperature measurements were averaged. To provide a conservative measure of DO concentrations in whedos, which are known to become hypoxic, we used the maximum recording to characterise DO in the habitats. For each habitat, per cent surface area coverage and height of aquatic macrophytes were estimated visually.

Analysis of fish assemblage structure

Variation in fish assemblage structure among habitats was examined using nonmetric multidimensional scaling (NMDS) ordination with two dimensions (k = 2) based on Bray-Curtis similarity matrices (Holland 2008). Because 2008 and 2009 data were presence–absence, all NMDS analyses were computed from species presence–absence data. Significant differences in assemblage structure were identified using one-way analysis of similarity (ANOSIM). We tested for significant differences in assemblage structure among whedo, natural floodplain depression and main channel habitats sampled in 2008, 2009 and 2010–2011. Because this ordination strongly differentiated between whedos versus the main channel and natural floodplain depression sites, the analysis was repeated with only data from whedos sampled in 2008, 2009 and 2010–2011 to evaluate assemblage structure of these habitats during different phases of the hydrological cycle. NMDS ordination also was performed on whedo data from the low-water period (2008 and 2009 samples) and the falling-water period (2010–2011) samples. For the 2010–2011 data, associations between habitat, physicochemical and fish CPUE data were explored using canonical correspondence analysis (CCA, Braak & Verdonschot 1995). Significant associations at $p < 0.05$ were identified using Bartlett's test. The software program PRIMER-E version 5 was used to perform NMDS and ANOSIM analyses, and the program PCORD was used to perform CCA analyses.

Results

Physicochemical variables–2010/2011

Dimensions of whedos sampled ranged from 39 to >1000 m (average = 595 m) in length, 4 to 6.3 m (average = 5 m) in width and 0.39 to 1.3 m (average = 0.78 m) in maximum depth (Table 1). Most (73%) of the whedo samples were $\geq 95\%$ covered in aquatic vegetation that was on average 90.7 cm in height above the water surface. Dominant aquatic macrophytes were *Leersia hexandra, Polygonum salicifolium, Ipomea aquatica* and *Aeschynomene afraspera*.

Dissolved oxygen concentrations were much lower in whedos (range ≤ 0.2 to 0.8 mg/L) compared with

Table 1. GPS coordinates and dimensions of all habitats measured in 2010–2011. Natural floodplain depression = floodplain. Because of the large size and irregular dimensions of the natural floodplain depression, length and width were not measured.

Habitat	GPS coordinates	Approximate Length (m)	Width (m)	Maximum depth (m)
Whedo 1	N 6° 41.853′, E 02° 28.212′	1000	5.0	1.3
Whedo 2	N 6° 41.701′, E 02° 28.185′	100	5.8	1.2
Whedo 3	N 6° 41.620′, E 02° 28.319′	1000	5.4	0.4
Whedo 4	N 6° 41.600′, E 02° 28.264′	500	4.6	0.9
Whedo 5	N 6° 41.577′, E 02° 28.267′	450	4.0	0.6
Whedo 6	N 6° 41.544′, E 02° 28.235′	450	6.3	1.0
Whedo 7	N 6° 41.674′, E 02° 28.272′	500	5.5	0.7
Whedo 8	N 6° 41.591′, E 02° 28.271′	1000	4.1	0.8
Whedo 9	N 6° 41.549′, E 02° 28.321′	500	4.8	0.6
Whedo 10	N 6° 41.458′, E 02° 28.308′	1000	4.8	0.4
Whedo 11	N 6° 41.431′, E 02° 28.223′	39	4.7	0.8
Floodplain	N 6° 41.422′, E 02° 28.204′	N/A	N/A	1.3
Main channel	N 6° 42.104′, E 02° 28.537′	N/A	125	2.4

either the natural floodplain depression (maximum 3.0 mg/L) or main channel (maximum 6.0 mg/L). Specific conductivity was higher in whedos (mean = 212.7 μS/cm) compared with the natural floodplain depression (specific conductivity = 135 μS/cm) and main channel habitats (105 μS/cm). pH averaged 6.2 in the whedos, 6.4 in the natural floodplain depression and 6.9 in the main channel. Temperature ranged from 23 to 27°C in whedos and the natural floodplain depression, and temperature in the main channel was 30°C.

Fish assemblage structure

In 2008, during the low-water period, a total of 13 fish species representing nine families and 11 genera was collected in floodplain habitats. Whedos contained from seven to ten fish species with high overlap among sites (Table 2). Seven species representing five families were captured in the natural floodplain depression, 86% of which were also found in whedos. In contrast, 18 fish species representing 11 families were collected from the river channel of which only five (26%) were found in whedos. All whedos contained *Ctenopoma petherici*, *Parachanna obscura*, *Polypterus senegalus* and *Clarias agboyiensis*, and most whedos had *Erpetoichthys calibaricus* (89%), *Clarias gariepinus* (89%), *Brienomyrus niger* (67%) and *Parachanna africana* (67%), all of which possess adaptations for aerial respiration.

In 2009, 14 fish species representing 11 families and 12 genera were collected in floodplain habitats, with whedos yielding from 7 to 12 species. Nine fish species representing seven families were captured

Table 2. Percent occurrence of species collected from whedos during the low-water period in 2008 and 2009 and the falling-water period in 2010/2011.

			Low Water Period		Falling Water Period	
Order	Family	Species	% whedos present 2008	% whedos present 2009	% whedos present 2010/2011	% of total abundance 2010/2011
Lepidosireniformes	Protopteridae	*Protopterus annectens*	11	55	36	0.5
Polypteriformes	Polypteridae	Erpetoichthys calabaricus	89	55	55	0.6
Polypteriformes	Polypteridae	*Polypterus senegalus*	100	100	100	5.4
Osteoglossiformes	Arapaimidae	*Heterotis niloticus*	22	64	0	0
Osteoglossiformes	Mormyridae	*Brienomyrus niger*	67	64	91	5.5
Osteoglossiformes	Mormyridae	*Mormyrus rume*	11	0	0	0
Osteoglossiformes	Notopteridae	*Xenomystus nigri*	44	55	36	0.8
Characiformes	Hepsetidae	*Hepsetus odoe*	0	27	0	0
Siluriformes	Clariidae	*Clarias agboyiensis*	100	100	100	55.8
Siluriformes	Clariidae	*Clarias gariepinus*	89	100	64	4.3
Siluriformes	Clariidae	*Gymnallabes typus*	0	0	18	0.2
Siluriformes	Malapteruridae	*Malapterurus beninensis*	11	0	18	0.2
Perciformes	Anabantidae	*Ctenopoma petherici*	100	100	100	22.1
Perciformes	Channidae	*Parachana africana*	67	55	18	0.4
Perciformes	Channidae	*Parachana obscura*	100	100	100	4.1
Perciformes	Cichlidae	*Hemichromis fasciatus*	0	0	9	0.1
Perciformes	Cichlidae	*Oreochromis niloticus*	0	27	9	0.1
Perciformes	Cichlidae	*Sarotherodon galilaeus*	0	9	9	0.1

from the natural floodplain depression, 89% of which were also found in whedos. In contrast, 17 fish species representing 11 families were collected from the river channel, of which only five (28%) were collected in whedos. All whedos contained the species *Ctenopoma petherici*, *Parachanna obscura*, *Polypterus senegalus*, *Clarias agboyiensis* and *Clarias geriepinus,* and most whedos contained *Heterotis niloticus* (64%), *Brienomyrus niger* (64%), *Protopterus annectens* (55%)*, Xenomystus nigri* (55%), *Parachana africana* (55%) and *Erpetoichthys calabaricus* (55%).

In 2010–2011, during the falling-water period, 1,831 fish specimens representing nine families, 13 genera and 15 species were collected from whedos. Whedos contained from 61 to 353 (average = 166) individuals and from six to nine (average = 7.6) species, with high species overlap among sites. A total of 131 specimens representing 11 families and 13 species were collected from the natural floodplain depression. Seven (54%) of the species caught in the natural floodplain depression also were found in whedos (47% of the total species in whedos). In contrast, a total of 434 specimens were collected from the river channel, representing 18 families and 33 species of which only four (12%) were found in the whedos. All whedos contained the species *Ctenopoma petherici*, *Parachanna obscura*, *Polypterus senegalus* and *Clarias agboyiensis*, and most whedos contained *Brienomyrus niger* (91%), *Clarias gariepinus* (64%) and *Erpetoichthys calibaricus* (55%). CPUE for whedos ranged from 0.75 to 6.1 individuals/m^3; CPUE was 0.8 individuals/m^3 in the natural floodplain depression and 1.79 individuals/m^3 in the river channel (Table 3). Total biomass per unit volume ranged from 18 to 172 g/m^3 in the whedos, and was 1.1 g/m^3 in the natural floodplain depression, 60.6 g/m^3 in the river-channel akadjavi and 18.3 g/m^3 in the river channel open water sampled with the cast net.

NMDS (k = 2) comparing assemblage structure among whedo, natural floodplain depression and main channel habitats sampled in 2008, 2009 and 2010–2011 (based on species presence–absence data) yielded an ordination with a 'good' stress value of 0.09 (Fig 2). ANOSIM indicated that whedos were significantly different from the natural floodplain depressions (R = 0.731, $p = 0.002$) and the main channel (R = 0.997, $p = 0.001$). In comparing assemblage structure among whedos sampled in 2008, 2009 and 2010–2011, NMDS (k = 2) generated an ordination with a 'fair' stress value of 0.16 (Fig 2). Whedo assemblages in 2008 were not significantly different from those in 2009 (ANOSIM, R = 0.053, $p = 0.216$) or 2010–2011 (R = 0.081, $p = 0.125$). However, whedos sampled in 2009 had significantly different fish assemblage structure than whedos sampled in 2010–2011 (R = 0.205, $p = 0.008$), and whedo fish assemblages during the low-water period (Feb. 2008 and Mar. 2009) were significantly different than those during the falling-water period (Dec. 2010 Jan. 2011) (ANOSIM, R = 0.173, $p = 0.015$).

Canonical correspondence analysis (CCA) of fish CPUE and six environmental variables collected in 2010–2011 in whedo, natural floodplain depression and river channel habitats yielded three pairs of canonical axes explaining 59.4% of variation in the dataset (Figs 3 and 4). Environmental axis 1 discriminated physicochemical differences among whedo, natural floodplain depression and main channel habitats, whereas environmental axis 2 discriminated among whedos. Environmental axis 1 explained 43.8% of the variance and contrasted whedos with higher % vegetation cover and specific conductivity with the natural floodplain depression and main channel habitats having higher maximum depth, temperature, pH and DO. Environmental axis 2 explained 11.7% of the variance and contrasted whedos with higher maximum depth, temperature and pH with whedos having higher specific conductivity. Whedos with greater depth, temperature and pH were dominated by the species *Brienomyrus niger*, *Clarias gariepinus*, *Ctenopoma petherici*, *Parachanna obscura*, *Polypterus senegalus* and *Xenomystus nigri*. Whedos with greater specific conductivity tended to contain higher densities of *Clarias agboyiensis*, *Erpetoichthys calabaricus, Gymnallabes typus*, *Malapterurus beninensis*, *Parachanna africana* and *Protopterus annectens*.

Discussion

The objective of this study was to test the relevance of metacommunity models for fish assemblage structure of shallow floodplain habitats of the lower Oueme River. Whedos sampled in 2008, 2009 and 2010–2011 were compared to test for differences in fish assemblage structure between hydrological periods (falling vs. low-water) and for correlations between assemblage structure and abiotic environmental conditions within habitats. Habitat types were distinct with regard to assemblage structure and abiotic conditions. Significant correlations existed between aspects of assemblage structure and physicochemical parameters.

If assemblage structure in the floodplain habitats results only from stochastic dispersal during the flood pulse, then high overlap would be expected between the main channel and floodplain habitats in assemblage ordination plots. This was not the case. Although there was a small amount of overlap, fish assemblages in the main channel and floodplain were distinct in that 66% of the 44 species found in the main channel were not found in samples from the floodplain (i.e., both the whedos and natural flood-

Table 3. Abundance catch-per-unit-effort (CPUE) of species collected from whedo, natural floodplain depression (floodplain) and river main channel habitats during the falling-water period in 2010-2011.

Order	Family	Species	Average whedo CPUE	Floodplain CPUE	Main channel CPUE
Lepidosireniformes	Protopteridae	*Protopterus annectens*	<0.1	0	0
Polypteriformes	Polypteridae	Erpetoichthys calabaricus	<0.1	0	0
Polypteriformes	Polypteridae	*Polypterus endlicheri*	0	0	<0.1
Polypteriformes	Polypteridae	*Polypterus senegalus*	0.1	<0.1	0
Osteoglossiformes	Mormyridae	*Brienomyrus niger*	0.1	<0.1	<0.1
Osteoglossiformes	Mormyridae	*Hyperopisus bebe*	0	0	<0.1
Osteoglossiformes	Mormyridae	*Mormyrops anguilloides*	0	0	<0.1
Osteoglossiformes	Mormyridae	*Mormyrus rume*	0	0	<0.1
Osteoglossiformes	Mormyridae	*Pollimyrus isidori*	0	0	0.2
Osteoglossiformes	Notopteridae	*Xenomystus nigri*	<0.1	0	0
Clupeiformes	Clupeidae	*Pellonula leonensis*	0	0	<0.1
Cypriniformes	Cyprinidae	*Labeo brachypoma*	0	0	<0.1
Characiformes	Alestidae	*Brycinus longipinnis*	0	<0.1	<0.1
Characiformes	Alestidae	*Brycinus macrolepidotus*	0	0	0.2
Characiformes	Alestidae	*Brycinus nurse*	0	0	<0.1
Characiformes	Alestidae	*Hydrocynus vittatus*	0	0	<0.1
Characiformes	Distichodontidae	*Distichodus rostratus*	0	0	<0.1
Characiformes	Distichodontidae	*Neolebias unifasciatus*	0	<0.1	0
Characiformes	Hepsetidae	*Hepsetus odoe*	0	<0.1	<0.1
Siluriformes	Bagridae	*Bagrus docmak*	0	0	<0.1
Siluriformes	Clariidae	*Clarias agboyiensis*	1.2	<0.1	0
Siluriformes	Clariidae	*Clarias gariepinus*	0.1	<0.1	0
Siluriformes	Clariidae	*Gymnallabes typus*	<0.1	0	0
Siluriformes	Clariidae	*Heterobranchus longifilis*	0	0	<0.1
Siluriformes	Claroteidae	*Chrysichthys aluuensis*	0	0	<0.1
Siluriformes	Claroteidae	*Chrysichthys ogooensis*	0	0	<0.1
Siluriformes	Malapteruridae	*Malapterurus beninensis*	<0.1	0	0
Siluriformes	Mochokidae	*Synodontis schall*	0	0	0.6
Siluriformes	Mochokidae	*Synodontis velifer*	0	0	<0.1
Siluriformes	Schilbeidae	*Schilbe intermedius*	0	0	0.1
Cyprinodontiformes	Nothobranchiidae	*Aphyosemion bitaeniatum*	0	0.1	0
Cyprinodontiformes	Poeciliidae	*Gambusia sp.*	0	<0.1	0
Synbranchiformes	Mastacembelidae	*Mastacembelus praensis*	0	0	<0.1
Perciformes	Cichlidae	*Tilapia guineensis*	0	0	0.1
Perciformes	Cichlidae	*Tilapia mariae*	0	0	<0.1
Perciformes	Eleotridae	*Eleotris senegalensis*	0	0	<0.1
Perciformes	Anabantidae	*Ctenopoma petherici*	0.5	<0.1	<0.1
Perciformes	Channidae	*Parachana africana*	<0.1	0	0
Perciformes	Channidae	*Parachana obscura*	0.1	<0.1	<0.1
Perciformes	Cichlidae	*Chromidotilapia guntheri*	0	0	0.3
Perciformes	Cichlidae	*Hemichromis fasciatus*	<0.1	0	0.1
Perciformes	Cichlidae	*Oreochromis niloticus*	<0.1	<0.1	0
Perciformes	Cichlidae	*Sarotherodon galilaeus*	<0.1	0	<0.1
Perciformes	Cichlidae	*Sarotherodon melanotheron*	0	0	<0.1
Perciformes	Cichlidae	*Tilapia cessiana*	0	0	<0.1

plain depressions). Furthermore, 96% of the individuals captured from the main channel in 2010–2011 were absent within samples from floodplain habitats. Fish assemblage structure was distinct in natural floodplain depression and whedo habitats, with only 7 (28%) of the 25 species found in the natural depression also occurring in whedos. Assemblages in whedos and natural floodplain depressions were differentiated from those of the main channel by domination of fishes that can tolerate conditions of low dissolved oxygen in floodplain habitats (72% of species in whedos, 61% in natural floodplain depressions and 23% in the main channel).

The fishes that dominated the communities of the whedos in both the falling and low-water periods possess adaptations for accessory or, in the case of the *Protopterus annectens* (the African lungfish), obligatory aerial respiration (Graham 1997). For example, the species *Ctenopoma petherici*, *Parachanna obscura* and *Parachanna africana* possess paired suprabranchial chambers that harbour labyrinth structures covered with respiratory epithelium (Munshi 1962; Liem 1984, 1987; Pinter 1986). The African lungfish is an obligatory air breather that possesses a pair of lungs that developed from an outpocketing of the gut, and can aestivate within a

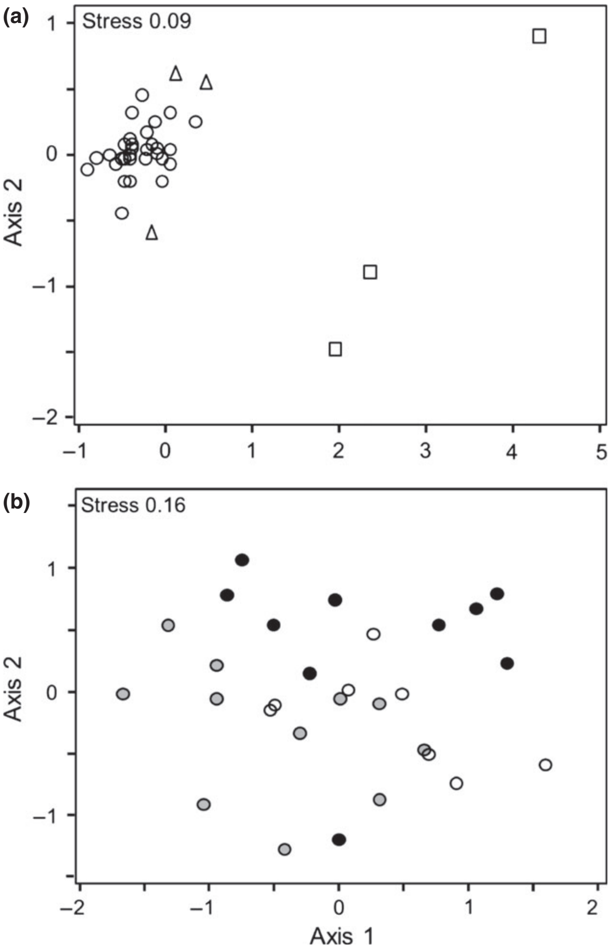

Fig. 2. Nonmetric multidimensional scaling analysis (NMDS) comparing assemblage structure (presence-absence data) among a) whedo (circle), natural floodplain depression (triangle) and main channel (square) habitats sampled in 2008, 2009 and 2010–2011, and b) whedo habitats sampled in 2008 (open circle), 2009 (grey circle) and 2010–2011 (black circle).

mucus cocoon buried in the ground for as long as 4 years (Parker 1892; Smith 1931; Johnels & Svensson 1954; Lomholt 1993). The catfishes *Clarias agboyiensis* and *Clarias gariepinus* possess aborescent organs in the branchial cavity that are covered by modified vascularised epithelium (St. Hilaire 1802a; Munshi 1967). Although its air-breathing organ has yet to be identified, aerial respiration has been observed in the mormyrid *Brienomyrus niger* (Benech & Lek 1981; Moritz & Linsenmair 2007). The osteoglossiforms *Xenomystus nigri* and *Heterotis niloticus* can absorb oxygen from air using a gas bladder lined with highly vascularised epithelium (Hyrtl 1854; Greenwood 1963). The bichirs *Erpetoichthys calabaricus* and *Polypterus senegalus* use highly-furrowed, paired lungs for aerial respiration (St. Hilaire 1802b; Purser 1926). In addition to having adaptations for aerial respiration, fishes of the families Clariidae, Channidae, Anabantidae and Protopteridae are known to survive dry periods by burrowing in mud to retain moisture and by moving over land in search of habitat (Day 1877; Smith 1931; Johnels 1957; Donnelly 1973; Pinter 1986; Pace & Gibb 2011).

Large differences in physicochemical conditions in river channel and floodplain habitats provided a foundation for species sorting based on environmental filtering. Dissolved oxygen concentrations in the whedos (range ≤ 0.2 to 0.8 mg/L) and natural floodplain depression (≤ 3.0 mg/L) were much lower than those recorded in the main channel (≤ 6.0 mg/L). Water temperatures in the whedos and floodplain were generally lower than those measured in the main channel, which makes DO differences even more notable. These observations run counter to the physical relationship between DO saturation and temperature. Low DO in the whedos was caused by the high densities of floating aquatic macrophytes (average coverage 94%). These die and decompose, inhibit gas exchange at the surface of the water and hinder algal photosynthesis by limiting light availability through shading (Rose & Crumpton 1996; Killgore & Hoover 2001). In the natural floodplain depression, aquatic macrophyte coverage was less than in the whedos, but still 50%. There also were differences in pH, specific conductivity and depth among floodplain habitats; however, the dominance of fishes with adaptations for aerial respiration in whedo assemblages indicates that dissolved oxygen was the predominant environmental filter structuring communities in these habitats. Little difference was observed in assemblage structure in whedos between the low and falling-water periods; however, fish assemblages from the natural floodplain depression revealed significant divergence between hydroperiods. Only 44% of the species found in the natural floodplain depression were present during both hydroperiods, with a higher percentage of fishes in the low-water period (85%) being tolerant to hypoxia compared with the falling-water period (61%). In whedos, 72% of species were present during both hydroperiods. This was likely because of the fact that in the whedos, dense coverage of aquatic macrophytes and low DO concentrations were already present during the initial stages of the falling-water period. The patterns observed in the natural floodplain habitats may be because of decline in DO as aquatic macrophyte biomass increased, or because of evaporative loss that caused temperatures to increase as water depth and surface area decreased with the progression of the dry season.

Findings from the Oueme River are consistent with similar studies that have documented a deterministic relationship between abiotic environmental variables and community structure in aquatic floodplain habitats (Winemiller 1989; Chapman & Liem 1995;

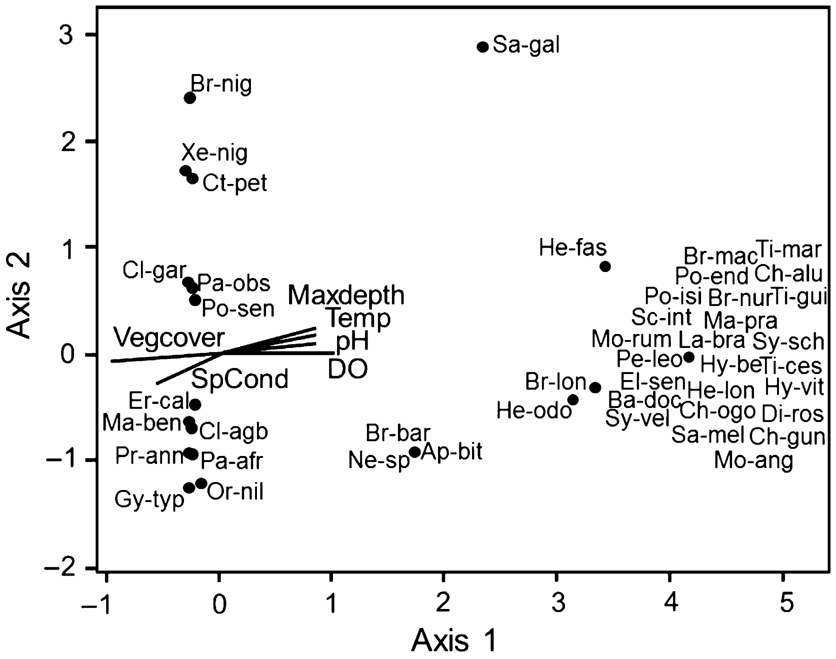

Fig. 3. Canonical correspondence analysis (CCA) of fish catch-per-unit-effort (CPUE) in the whedo, natural floodplain depression and main channel habitats and six physicochemical variables collected in 2010/2011. Dissolved oxygen = DO, specific conductivity = SpCond, temperature = Temp, per cent surface area coverage of aquatic macrophytes = VegCover and maximum depth = MaxDep. Ap-bit = *Aphyosemion bitaeniatum*, Ba-doc = *Bagrus docmak*, Br-nig = *Brienomyrus niger,* Br-bar = *Brycinus longipinnis*, Br-mac = *Brycinus macrolepidotus*, Br- nur = *Brycinus nurse*, Ch- gun = *Chromidotilapia guntheri*, Ch-alu = *Chrysichthys aluuensis*, Ch-ogo = *Chrysichthys ogooensis*, Cl-agb = *Clarias agboyiensis*, Cl-gar = *Clarias gariepinus*, Ct-pet = *Ctenopoma petherici,* Di-ros = *Distichodus rostratus*, El-sen = *Eleotris senegalensis*, Er-cal = *Erpetoichthys calabaricus*, Ga-sp. = *Gambusia* sp., Gy-typ = *Gymnallabes typus*, He-fas = *Hemichromis fasciatus*, He-odo = *Hepsetus odoe*, Hy-vit = *Hydrocynus vittatus*, He-lon = *Heterobranchus longifilis*, Hy-be = *Hyperopisus bebe*, La-bra = *Labeo brachypoma*, Ma-ben = *Malapterurus beninensis*, Ma-pra = *Mastacembelus praensis*, Mi-elo = *Micralestes elongatus*, Mo-ang = *Mormyrops anguilloides*, Mo-rum = *Mormyrus rume*, Ne-uni = *Neolebias unifasciatus*, Or-nil = *Oreochromis niloticus*, Pa-afr = *Parachana africana*, Pa-obs = *Parachana obscura,* Pe-leo = *Pellonula leonensis*, Po-isi = *Pollimyrus isidori*, Po-end = *Polypterus endlicheri*, Po-sen = *Polypterus senegalus*, Pr-ann = *Protopterus annectens*, Sa-gal = *Sarotherodon galilaeus*, Sa-mel = *Sarotherodon melanotheron*, Sc-int = *Schilbe intermedius*, Sy-sch = *Synodontis schall*, Sy-vel = *Synodontis haugi*, Ti-ces = *Tilapia cessiana*, Ti-gui = *Tilapia guineensis*, Ti-mar = *Tilapia mariae* and Xe-nig = *Xenomystus nigri*.

Winemiller et al. 2000; Killgore & Hoover 2001; Hoeinghaus et al. 2003; Petry et al. 2003b). For example, Chapman & Liem (1995) found that in the Njuguta River in Uganda, hypoxic floodplain habitats with dense coverage of aquatic macrophytes at the water surface had fewer nonair breathing fishes than habitats with large areas of open water at the surface. Winemiller et al. (2000) found that in the floodplain of the Brazos River in Texas, USA, shallow oxbow lakes with high densities of aquatic macrophytes experienced reduced levels of wind mixing, phytoplankton biomass and DO that resulted in lower fish species diversity. Furthermore, studies frequently show that hypoxia is an ecological barrier in that it limits the dispersal of fishes between aquatic habitats (Roberts 1975; Kramer 1983, 1987; Suthers & Gee 1986; Saint- Paul & Soares 1987).

Biotic interactions also affect fish assemblage structure in river floodplain habitats (Lowell-McConnell 1964; Robinson & Tonn 1989; Rodriguez & Lewis 1997). For example, in the drying lagoons of the upper Parana ́ River floodplain in Brazil, community structure is strongly influenced by abiotic environmental variables as well as predation and competition as lagoons shrink and resources become limited (Okada et al. 2003; Petry et al. 2003a). Predator–prey interactions probably influence species assemblage structure in floodplain habitats of the Oueme River. During the falling and low-water periods, most fishes in the whedos and natural floodplain depressions sampled were piscivores. Predation has been inferred to drive community changes in floodplain habitats as the water level falls and fish densities increase (e.g., Lowell-McConnell 1964; Winemiller 1990). For example, Montaña et al. (2011) found that on the floodplains of the Cinaruco, La Guardia and Ventuari rivers of Venezuela, as habitats shrink during the dry season, there is a shift in the trophic structure of fish assemblages from domination by herbivores and invertivores to domination by piscivores. Several studies have shown that the presence of piscivorous fish affects community structure, with prey species selecting habitats that provide refuge from predation (e.g., Werner et al. 1983;

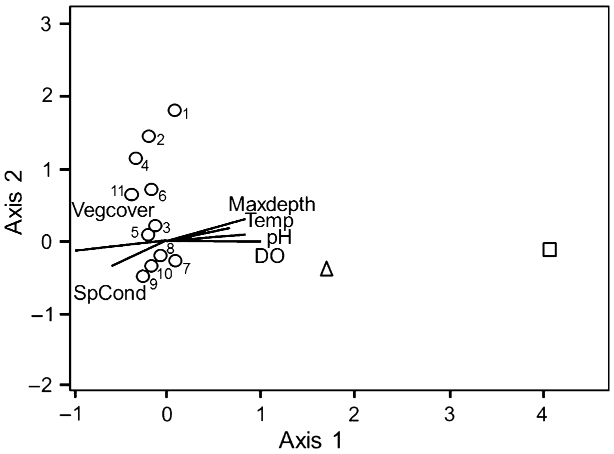

Fig. 4. Canonical correspondence analysis (CCA) of fish catch-per-unit-effort (CPUE) in whedo (circle), natural floodplain depression (triangle) and main channel (square) habitats collected in 2010/2011 and vectors revealing axis loadings of six physicochemical variables. Codes for vectors are defined in Fig. 3.

Schlosser & Angermeier 1990; Harvey 1991; Gilliam & Fraser 2001; Layman & Winemiller 2004). In the isolated aquatic habitats of the Oueme River floodplain, however, it seems unlikely that prey species would be able to avoid predation through habitat selection at the local scale. This is because low DO forces fishes that cannot breathe air to spend more time at the surface performing aquatic surface respiration that increases risk of predation (Kramer et al. 1983; Chapman & Liem 1995).

The neutral model of metacommunity dynamics can be rejected for fish assemblages in aquatic floodplain habitats of the lower Oueme River. However, each of the other three metacommunity models is consistent with aspects of these fish assemblages. The natural floodplain depression had a more diverse fish assemblage during the falling-water period when several species lacked obvious adaptations for accessory aerial respiration. During the low-water period, most fishes in the natural and human-constructed floodplain habitats were piscivores tolerant of hypoxia. Following colonisation of these habitats during the flood pulse, fishes that lack accessory respiratory adaptations and that were vulnerable to piscivores apparently were eliminated. This scenario is consistent with the patch dynamics model. After the flood pulse subsides, floodplain habitats become isolated and remain so until fishermen harvest them. Consistent with the mass effect model, fish communities of floodplain habitats can be explained in part by a source (river channel)-sink (floodplain) dynamic whereby fishes are able to persist in a hostile habitat because of immigration from a more favourable habitat. In this floodplain ecosystem, harsh environmental conditions in isolated floodplain habitats result in local assemblages that are subsets of regional fish diversity and dominated by predatory species resistant to aquatic hypoxia. This suggests that stochastic colonisation of the floodplain followed by environmental filtering (species sorting), predation (patch dynamics) or a combination of both mechanisms influence species assemblage structure at the local scale.

In a conceptual synthesis of community ecology, Vellend (2010) stated that the four metacommunity models ‘do not represent logically distinct classes of ecological processes.’ Indeed, three of the metacommunity models could be invoked to describe the patterns of fish assemblage structure that we observed. Vellend (2010) argued that all community patterns can be understood based on just four processes: selection, drift, speciation and dispersal. Our findings suggest that of these four processes, selection (i.e., filtering of species by hypoxia and/or predation) and dispersal (i.e., colonisation of the floodplain by fishes from the river channel during seasonal floods) play the most prominent roles in shaping local community structure in aquatic habitats of the Oueme River and floodplain. None of the metacommunity models fully explains fish assemblage structure, and the framework proposed by Vellend (2010) more closely captures the processes producing patterns in this system.

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