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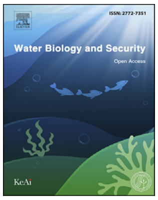

Land-use and land-cover affect inland fish catch in two rivers of Central Africa

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ABSTRACT

Land-cover change can affect inland fisheries, which underpin food security of millions of people worldwide. Removal of forests from very large floodplains has been found to decrease fish catch via loss of feeding and nursery habitat for fish. However, it is unknown if similar effects occur in smaller rivers with limited floodplain areas. Little is also known about the mechanisms by which land-cover changes affect inland fish catch. Here, we assessed land-use and land-cover (LULC) effects on fish catch, diet, and condition at sites in two medium-sized rivers of Cameroon, in Central Africa. We found that LULC explained 30% of the variation in fish catch, with the catch of five species being positively, and of two species being negatively, related to floodplain forests. The niche breadth of fish diets was higher in the river surrounded by forests than in the river surrounded by agricultural land. However, contrary to expectations, condition of the fish, as indicated by occurrence of diseases or deformities, eroded fins, lesions or tumors, was not related to LULC. Our results support the notions that floodplain forests support fish populations in rivers with limited floodplain areas in ways similar to that of rivers with large floodplains, and that LULC affects fish populations via changes in fish diets and instream habitat features (i.e., riparian canopy closure, water clarity, substrate heterogeneity, and habitat volume). These effects imply that prevailing changes in LULC threaten the food and livelihood security services provided by inland fisheries, highlighting the importance of policies that maintain native vegetation along riverbanks and in floodplain areas.

1. Introduction

Resource use activities such as agriculture or cattle ranching are promoted worldwide as pillars of economic development strategies (Foley et al., 2005; Lambin and Meyfroidt, 2011). These activities lead to land-cover changes that conflict with other resource uses such as inland fisheries, which underpin the food security of millions of people, mainly in the tropics where demand for food (especially protein) and habitat modification are increasing (Welcomme et al., 2010). The most productive inland fisheries occur in river floodplain ecosystems where vegetated habitats provide critical habitat for fish (Bayley, 1995; Castello et al., 2018, 2019). However, little is known about how land-use and land-cover (LULC) change affect inland fish catch. This is so because of a dearth of research on the topic and the difficulty of quantifying the effects of LULC change on fish catch when land cover changes often occur together with other development activities, such as dam construction and hydrological alteration (e.g., Scarabotti et al., 2021). This current lack of understanding of LULC effects on fish catch makes it difficult for policy makers to assess the potential costs and benefits of resource use options.

River fish catch depends on hydrology and floodplain vegetation. Seasonally rising river waters prompt fish to spawn and migrate out of river channels onto the vegetated habitats of the floodplains, where fish benefit from shade that maintains water temperature and structural complexity that provides protection against predators and filters terrestrial runoff (Lo et al., 2020). In these environments, fish also benefit from abundant food resources, including tree seeds, fruits, leaves, aquatic and

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terrestrial invertebrates, and detritus that increase their rates of survival and somatic growth (Castello, 2008; Gomes and Agostinho, 1997). C_3 plants (e.g., trees) and algae are key sources of carbon supporting fish biomass (Oliveira et al., 2006; Ou and Winemiller, 2016). Floodplain forest area thus tend to be positively related to fish abundance, biomass, and catch, although fish responses to habitat depend on their life history traits (Arantes et al., 2018, 2019; Castello et al., 2018; Welcomme, 1985, 1995).

Previous studies assessing LULC effects on fish catch were done in very large rivers that possess huge floodplains areas (Lo et al., 2020). In the Amazon River, for example, where several fish-forest linkages have been established, floodplain areas can be up to tens of kilometers wide, possessing a diversity of habitats, including forests, shrubs, grasslands, lakes and connecting channels (Hess et al., 2015). However, how floodplain forests affect fish abundance and biomass in small or medium-sized rivers, which possess floodplain areas that are only tens or hundreds of meters wide, remains uncertain due to a lack of studies. Also, mosaics of environments formed by backwaters, rapids, and tributary mouths have been shown to play critical roles for young fish in rivers without floodable areas (Lopes and Zaniboni-Filho, 2019), suggesting that fish also adapt to the lack of floodplain habitats. Food resources in backwater and littoral environments have been shown to be important for young fish in rivers with limited floodplain areas (King, 2004). In the absence of allochthonous food resources, autochthonous production is a key source of energy (Flecker et al., 2002; Thorp and Bowes, 2017; Silva et al., 2020). Therefore, although floodplain habitats are key to many fishes (Dale Jones III et al., 1999), the more limited riparian areas of small or medium-sized rivers may exert limited effects on fish biomass and abundance or be associated with fish life history traits that are less dependent on such habitats.

Questions also remain about the processes by which changes in LULC affect fish abundance and biomass. As natural forests are lost, decreases in availability and quality of food are expected to affect fish diets. However, the diets of many freshwater fishes naturally vary with age, season, and location within the system (Carvalho et al., 2018; Vadas et al., 2022; Welcomme et al., 2006; Winemiller et al., 2014). Fish may thus be able to adapt their feeding behaviors to the grassy vegetation that typically follows deforestation, with no or limited effects on their biomass or abundance (Arantes et al., 2019a,b; Melo et al., 2019). Changes in LULC can also be expected to affect fish abundance and biomass via changes in host–pathogen systems (Hall et al., 2009; Johnson et al., 2007). Stress produced by habitat changes (e.g., dissolved oxygen) has been shown to affect the susceptibility of fish to infectious diseases (Wedekind et al., 2010). In particular, organic enrichment of aquatic environments, which can occur via soil erosion following deforestation, often leads to increased risk of infection, as observed in various kinds of pathogenic agents (e.g., helminth, myxozoan, bacterial, fungal, and viral pathogens; McKenzie and Townsend, 2007). However, while it would seem that LULC can affect fish diet and condition, thereby explaining LULC effects on fish populations in river floodplains, the topic remains poorly studied.

Here, to foster understanding of how LULC affect inland fish catch, we assessed possible linkages between fish catch, diet, and condition with floodplain forest and associated LULC in two medium-sized rivers of Cameroon, in Central Africa. We addressed three research questions related to whether floodplain forests are related to (1) fish abundance and biomass, (2) fish diet, and (3) fish condition. We collected fish catch and fishing habitat data and modeled fish catch by biomass and abundance in different fishing sites along the two rivers as a function of river morphology, forest cover, and habitat variables. We also compared fish diet and fish condition between the two rivers, based on marked forest cover differences between the rivers.

2. Methods

2.1. Study area

Our study area was the East Region of Cameroon, specifically in the Kadey and Boumba Rivers (Fig. 1). The climate in this area falls within the tropical savanna (Aw) and tropical monsoonal (Am) climates according to the Koppen-Geiger climate classification (Peel et al., 2007). The climate is influenced by the hot and humid equatorial climate of the Guinean type (Suchel, 1987) with two distinct rainy seasons interspersed with two dry seasons. This includes a short rainy season from mid-March to June, followed by a short dry season from July to mid-August, followed by a main rainy season from mid-August to mid-November, followed by a main dry season from mid-November to mid-March (Suchel, 1987). This variability in rainfall causes the Kadey and Boumba rivers to follow a single dry (November to mid-April) and flood season (mid-April to October).

The East Region of Cameroon is covered in rain forest in the south and humid wooded savannah in the north. The Boumba River is located on the south of the East Region where rain forests dominate; it is nearly 530 km long and flows into the Dja River (Vivien, 2012). The Boumba River has a channel around 75 m wide and floodplain areas about 20 m wide dominated by forest vegetation, and a mean annual flow of 106 $m^3 \cdot s^{-1}$. The Kadey River is located on the north of the East Region, near the ecotone between rain forest and wooded savannah ecosystems (Fig. 1); it is a tributary of the Sangha River and part of the Congo River Basin. The Kadey River is 570 km long and has a mean annual flow of 247 $m^3 \cdot s^{-1}$, a channel around 100 m wide, and floodplain areas about 5–20 m wide dominated by mixed forest and agricultural land. Although the Kadey River appears to have been altered by land cover changes, we cannot determine the extent to which the relative absence of forests in the Kadey is natural or the result of land cover changes (e.g., due to agricultural expansion); it is likely a combination of both factors.

Within the Kadey and Boumba rivers, our study focused on four riverine communities, including the Biwala I and Biwala II communities on the Boumba River in the Ngoko District, and Sone and Mindourou

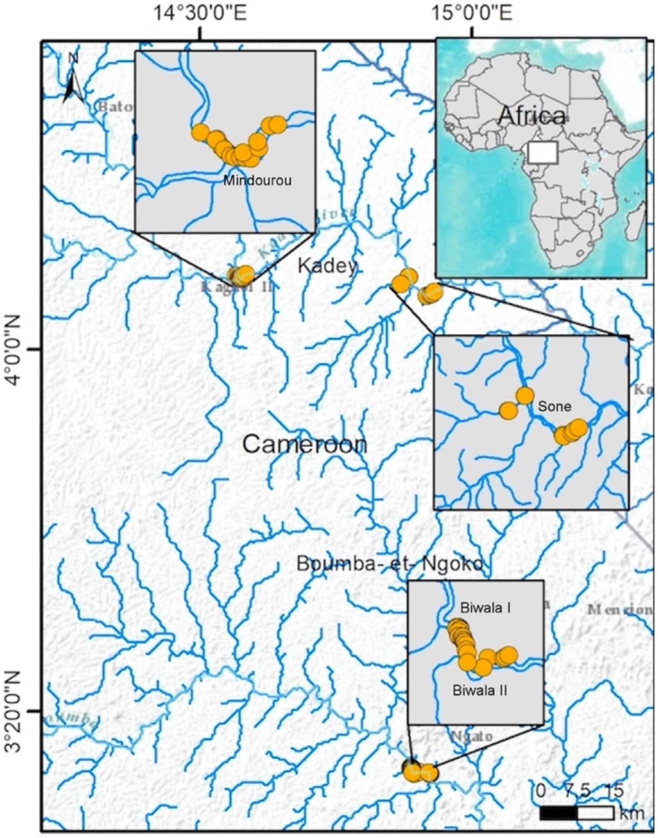

Fig. 1. Map of the study area in the East Region of Cameroon, showing the Boumba and Kadey rivers, habitat sampling sites, and the fishing communities.

communities along the Kadey River in the Commune de Ndelele District. Fishing is more prominent in the Kadey River communities, while Boumba River communities engage more in hunting. Fishing gear in both rivers typically included line hooks, gill-nets, traps, baskets, and cast nets, with fishing trips being conducted in dugout canoes by paddle and rarely lasting over one day.

2.2. Fish and habitat sampling

Establishing fish-forest relationships is difficult because it requires matching the spatial and temporal scales of the processes involved; this difficulty is thought to explain varied and inconsistent evidence on the effects of land cover changes on freshwater fish (Smokorowski and Pratt, 2007). Here, we used a space-for-time substitution approach in which we compared fish catch in forested and non-forested sites of the two rivers, as done in previous studies elsewhere (e.g., Arantes et al., 2019a,b; Castello et al., 2018). Given that there could be fisheries and habitat differences across the two rivers, we organized our study locations by two hierarchical spatial scales, the river basin and the reach. Thus, our analyses could assess fisheries and habitat characteristics in forested and non-forested sites while accounting for differences across rivers and fisheries. In our study, the Boumba and Kadey rivers represent the higher level of the hierarchy, whereas specific sampling sites (100–200 m long) within each river basin represent the lower level. Fisheries data and habitat measurements were made at the site scale.

Prior to sampling, we obtained permission from the two district offices to conduct this research. We then met with community leaders and explained the nature of our research, and asked for their consent to ask questions to fishers about their fishing activities. We received verbal consent from fishers; their participation in the study was voluntary. We sought to conduct interviews with all fishers at the time when they returned from fishing in all four communities. The interviews were done from late January to end of May 2019, spanning the dry and rainy season in both rivers, which comprised the bulk of the annual fishing season. Fishers were asked about which sites they fished, how long they fished, and what gear they used. Fishers were also asked about whether they fished in the middle of the site (midriver) or nearshore, depending on river morphology and availability of supporting structures of the gear. After obtaining fishers' permission, we recorded the taxa caught and weighed the specimens. For a sample of fishing trips, we purchased all specimens of all species caught by the fishers to examine their condition and gut contents.

Parallel with recording of fishing trips, we measured habitat characteristics of all 34 sites reported by the fishers in the two rivers (12 in Boumba and 22 in Kadey). For each site, we (i) recorded the latitude and longitude coordinates; (ii) classified the predominant channel geomorphic unit as pool, riffle, or run; (iii) measured mean flow using the float method where discharge was estimated from the velocity (estimated using a float), wetted width of the channel (perpendicular to shore measured with a tape measure), and depth (measured at across the width with a meter stick); and (iv) classified main substrate types, riparian vegetation, and LULC, all via visual observation. Due to the large extent of river areas and depths that were often not wadeable, qualitative habitat measurements were the only feasible option for most variables and also ensured that measurements were not represented as more accurate than they really are. Qualitative habitat evaluations have been used routinely as a component of rigorous, quantitative stream habitat assessments to understand fish-habitat relationships (e.g., Frimpong et al. 2005). For LULC, on-site observation was supplemented with aerial photo analysis of floodplain and non-floodplain areas using Google Earth. Substrate types were classified as clay, sand, gravel, or boulder. Floodplain vegetation was classified as grass or tree and floodplain canopy was classified as open, semi-open, or closed. Site LULC was classified as closed forest, agricultural, or mined or barren land in non-floodplain areas adjacent to each site. Field measurements of width was also verified in Google Earth and corrected if a discrepancy was found. We also measured water quality variables (dissolved oxygen, temperature, pH, conductivity, and turbidity) periodically at select locations in each cluster of sites in both rivers. Water quality was measured in-situ using a Sper Scientific model 850081DOK for dissolved oxygen; a multiparameter probe (PCSTestr 35) for temperature, pH, conductivity; and a secchi disc for turbidity.

We examined the purchased specimens with respect to their condition and gut contents at the University of Yaounde I, in Yaounde, Cameroon. Each specimen was rinsed thoroughly with water, encoded using a General Purpose Frigate tag, and weighed using a digital scale with 1 g precision. We used standardized methods for evaluating fish condition (Sanders et al. 1999), by examining the barbels, scales, fins, skin, opercula and eyes of each specimen for possible occurrence of Diseases (e.g., presence of parasites) or Deformities, Eroded fins, Lesions or Tumors (DELT), first with our naked eyes and then under stereo microscope (Olympus BO61). Each specimen was classified with respect to occurrence or absence of DELT. To analyze gut diet content, we opened the stomachs by incision, extracted and placed the contents in petri dishes, and rinsed through a sieve with a 25 μm diameter mesh. We sorted the items retained on the sieves and the filtrate with our naked eyes and under a stereo microscope. We identified the diet contents to the lowest possible taxonomic group. We then counted and weighed each diet item using an electronic scale to the nearest mg.

Prior to analyses, we recoded data as appropriate for the statistical methods. For the fisheries and habitat data, we coded the habitat variables as continuous, dummy (0 = absence,1 = presence for factor), or a list of categories, depending on the analysis (see below). In all analyses we added dummy variables to represent the spatially clustered structure of the data belonging to the two rivers (i.e., Boumba cluster and Kadey cluster). We assumed that fishing may be selective for certain species depending on gear location; therefore, we accounted for this selectivity by including gear location when determining the predictors of individual species capture rates. To analyze habitat associations of species, we focused on a subset of 16 species that were captured in both the Boumba and Kadey Rivers and for which the fishing data were matched with data from at least one of the reaches (Fig. 2). We filtered the data to include only this subset of 16 species to ensure our analysis would not lead to misleading results. We calculated fish catch as catch per unit effort (CPUE) based on both abundance (number of specimens per number of hours fishing) and biomass (kg per number of hours fishing) of fish caught for each of the 16 species. CPUE was calculated only for fishing trips done with gillnets, to remove CPUE variability from different gears. We excluded four of the 22 surveyed habitat reaches from the Kadey River from our analyses, because the accuracy of their fish catch data was uncertain. We also excluded water quality data (dissolved oxygen, temperature, pH, and conductivity) because they showed no variability across sites. Overall, 30 reaches (12 Boumba, 18 Kadey) were included in the analyses of species-habitat relationships (Table 1).

2.3. Data analyses

Fish abundance and catch. To assess if species abundance was related to habitat, we used the Least Absolute Shrinkage and Selection Operator (LASSO)-regularized Poisson regression. The LASSO method simultaneously fits a generalized linear regression model and incorporates variable selection, allowing for the regression coefficients of non-significant variables to be shrunk to zero, thereby minimizing model overfitting and allowing the most important variables to be clearly identified (James et al., 2012). Because the LASSO method excluded some variables, the variables used in our modeling included a subset of all environmental variables measured in the field. We modeled abundance of each of the 16 species as a function of habitat characteristics, including the following candidate explanatory variables: river (Boumba or Kadey), average reach width (m), maximum reach depth (m), flow velocity ($m \cdot s^{-1}$), morphology (run or riffle = 1), substrate (clay = 1), substrate (sand = 1), substrate (rock or boulders = 1), floodplain LULC (open canopy = 1),

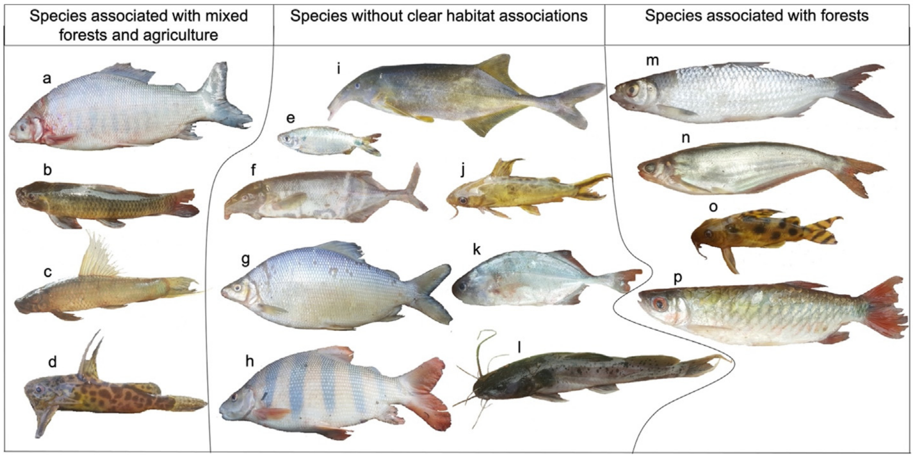

Fig. 2. The sixteen species shared between the Boumba and Kadey rivers in Cameroon, Central Africa, that were analyzed with respect to fish-habitat relationships. The species are grouped according to their habitat associations (see results). Species codes are as follows: (**a**) *Distichodus mossambicus*, (**b**) *Labeo lukulae*, (**c**) *Labeo macrostoma,* (**d**) *Synodontis greshoffi,* (**e**) *Brycinus imberi,* (**f**) *Marcusenius mento,* (**g**) *Distichodus affinis,* (**h**) *Distichodus sexfasciatus,* (**i**) *Campylomormyrus tamandua,* (**j**) *Synodontis pleurops,* (**k**) *Petrocephalus simus,* (**l**) *Bagrus ubangensis,* (**m**) *Alestes macrophthalmus,* (**n**) *Schilbe mystus,* (**o**) *Synodontis decorus,* (**p**) *Brycinus macrolepidotus.* Photos by G. A-T. Attu, A. Aliebe, N. O. Onana Ateba, and S. Jueya.

Table 1
Location and number of fishing trips included in analyses of species-habitat relationships in each of the two rivers.

River	Site ID	Lat (N)	Lon (E)	No. of fishing trips
Kadey	KAD01	04°08.270′	014°35.056′	12
	KAD02	04°08.252′	014°34.946′	12
	KAD03	04°08.034′	014°34.771′	6
	KAD04	04°07.941′	014°34.789′	70
	KAD05	04°07.803′	014°34.679′	11
	KAD06	04°07.807′	014°34.597′	5
	KAD07	04°07.814′	014°34.533′	10
	KAD08	04°07.817′	014°34.456′	10
	KAD09	04°07.837′	014°34.404′	4
	KAD10	04°07.929′	014°34.308′	3
	KAD11	04°08.066′	014°34.192′	3
	KAD12	04°08.174′	014°33.979′	30
	KAD13	04°07.845′	014°34.413′	11
	KAD14	04°07.907′	014°34.328′	10
	KAD15	04°07.963′	014°34.272′	7
	KAD16	04°08.074′	014°34.208′	1
	KAD17	04°06.336′	014°55.821′	1
	KAD18	04°06.149′	014°55.582′	2
Boumba	BOU01	03°13.317′	014°54.133′	4
	BOU02	03°13.282′	014°54.078′	1
	BOU03	03°13.257′	014°54.034′	1
	BOU04	03°13.699′	014°53.672′	1
	BOU05	03°13.269′	014°53.763′	8
	BOU06	03°13.698′	014°53.254′	4
	BOU07	03°13.607′	014°53.329′	1
	BOU08	03°13.237′	014°55.168′	5
	BOU09	03°13.205′	014°55.281′	4
	BOU10	03°13.166′	014°55.300′	4
	BOU11	03°13.115′	014°55.406′	1
	BOU12	03°13.079′	014°55.386′	1

reach LULC (closed forest = 1), and location (midriver = 1).

To complement the LASSO regressions, we assessed if CPUE by abundance and biomass simultaneously were related to habitat by performing an ordination of the species CPUE matrices followed by a fitting of the environmental (habitat) data matrix to the vectors retained in each ordination (Oksanen et al., 2013). We used non-metric multidimensional scaling (NMDS) with Bray-Curtis distances for species ordinations, accepting the default two-dimensional solution with minimum stress, and tested the significance of correlations of habitat variables with NMDS vectors using 9999 permutations. We developed ordination graphics (biplots) to aid in interpretation of the species-habitat relationships; although the species-habitat relationships identified by the LASSO modeling (site-scale) and the NMDS analysis (river-scale) differ in their spatial scales, we note the NMDS analysis was done for purposes of visualizing species-habitat relationships. Both LASSO regressions and ordinations were performed in R (R Core Team, 2020) using *glmnet* and *vegan* packages respectively.

Fish diet and condition. To assess if fish diet and condition were related to forests, we compared diet and condition descriptors between the two rivers, which had major differences in forest cover. We did this analysis at the river, not the site, level. We could not relate the specimen-level diet and condition to the site habitat characteristics because the data were not sufficiently spatially linked. Because of sample-size limitations, we conducted these analyses for only nine of the 16 species common to both rivers. To address our question of whether fish diet is related to floodplain forests, we estimated an index of niche breath (INB) for each fish species that was caught in both rivers. We calculated the INB for all individuals sampled in each river using the formula: $Bi = \frac{1}{n-1}\left[1/\left(\sum_i p_i^2\right) - 1\right]$, where B_i = the index for species *i*, p_{ij} the proportion of diet of each individual that is made up of food item *j* and *n* = the number of prey categories (Levins, 2020). INB values were set according to the following thresholds: high (>0.6), intermediate (0.4–0.6) and low (<0.4). Using the INB values, we ran a one-tailed *t*-test to test the hypothesis that the niche breadth of Boumba individuals was larger than that of Kadey individuals. We also estimated the relative contribution of terrestrial vegetation to the diet of each individual fish. We estimated the percentage of the stomach content in weight that was composed of terrestrial vegetation (leaves, flowers, fruits). Finally, to address our question of whether fish condition is related to floodplain forests, we used a Chi square goodness-of-fit test (Zar, 1999) to assess whether the proportion of individuals with DELT anomalies differed between the two river systems.

3. Results

3.1. Fish and habitat data

Habitat differed in several ways between rivers and across fishing sites within each river, with marked differences in LULC (Table 2). Sixty seven percent of fishing sites in the Boumba River were surrounded by closed forest with only 33% of the sites having partial canopy over the channel because of farming. In comparison, 100% of the sites in the Kadey River were surrounded by mixed forest and agricultural land, with 95% of them having open forest canopy over the channel naturally or because of farming (Table 2). Boumba sites had generally clearer water, with boulder substrate interspersed with sand and clay whereas sand and clay with embedded boulders dominated Kadey substrates. Compared with the Boumba, Kadey sites were wider and slightly deeper and had similar proportions of run and pool versus 75% pool; thus the Kadey sites had greater habitat volume and greater substrate heterogeneity (Table 2).

Table 2
Habitat characteristics of the 34 fishing sites sampled in the Kadey and Boumba Rivers. Shown are mean estimates and values in parenthesis are range (maximum–minimum).

Variable	Boumba River ($n = 12$)	Kadey River ($n = 22$)
Site land cover		
closed forest (%)	67	0
open forest with agriculture (%)	33	100
Floodplain condition		
closed canopy (%)	67	0
partial canopy (%)	33	95
open canopy	0	5
Geomorphic units		
pool (%)	75	55
run (%)	17	45
riffle (%)	8	0
Substrate		
boulder	50	14
sandy and boulder	17	32
sandy	17	36
clayey	8	0
Clayey and boulder	8	18
Morphology & velocity		
Average depth (m)	1.9 (0.5–2.9)	2.2 (0.7–4.0)
Maximum depth (m)	2.8 (0.8–4.2)	3.0 (0.8–5.8)
Width (m)	74 (39–125)	94 (55–163)
Width to depth ratio (unitless)	53 (19–255)	52 (18–108)
Velocity (m s^{-1})	0.34 (0.15–0.77)	0.32 (0–0.94)
Water quality		
Dissolved Oxygen (mg/L)	6.5 (2.6–16.9)	9.8 (6.0–12.6)
Temperature (°C)	25.6 (24.8–26.7)	26.5 (24.9–29.1)
pH	7.6 (6.8–8.7)	7.1 (6.5–7.7)
Transparency [Secchi depth (m)]	0.9 (0.7–1.1)	0.2 (0.1–0.4)

Fisheries in all sites possessed the characteristics of a typical artisanal, small-scale, tropical subsistence fishery. Fishing in the Kadey River appeared to be more intense than in the Boumba, as we recorded 401 fishing trips in the Kadey but only 44 in the Boumba in the same sampling period. CPUE in biomass and abundance in the Kadey were about an order of magnitude smaller than those in the Boumba (Table 3), possibly because of greater fishing effort. In total, we recorded the catch of 85 species in the Kadey and 33 in the Boumba, with the 10 top species contributing between half and 80% of the total catch in abundance or biomass (Table 3).

3.2. *Fish abundance and biomass relations with forests*

Fish abundance and biomass were clearly related to LULC and in particular to forests. For 12 of the 16 species modeled, the LASSO regressions retained at least one habitat variable besides the River and gear location variables. Seven of the 12 species showed relationships with LULC type including land cover in the surrounding landscape or riparian areas, and five or six showed direct dependence on closed forests (Table 4). Ten of the 12 species also showed relationships in at least two of the three broad categories of habitat variables used in the models (i.e., LULC, substrate, and river morphology/flow), allowing to examine in the discussion the consistency of associations of species' traits with the retained habitat variables. These results showing that LULC was frequently retained came along with other habitat variables showing positive or negative correlations with LULC. For example, closed forest was positively correlated with deep water and rocky substrate, whereas mixed forest and agriculture was correlated with stream that is wide and shallow with sandy substrate (Fig. 3). Our above interpretation, therefore, considered both the potential direct effect of LULC as well as the indirect effects of LULC on instream habitat structure. Eight species (*Labeo macrostoma*, *Distichodus mossambicus*, *Alestes macrophthalmus*, *Schilbe mystus*, *Labeo lukulae*, *Synodontis decorus*, *Brycinus macrolepidotus*, and *Synodontis greshoffi*) showed strong and potentially interpretable specific habitat relationships. For other species (*Petrocephalus simus*, *Marcusenius mento*, *Brycinus imberi*, and *Distichodus sexfasciatus*), the relationships with habitat were driven primarily by a single variable, having patterns that were difficult to separate from potential statistical artifacts due to insufficient number of observations across one or both rivers.

Table 3
Key characteristics of fishing trips recorded in the Kadey and Boumba rivers.

Fisheries characteristics	Boumba	Kadey
Total number of species (n)	33	85
Average catch biomass (kg) per fishing trip	2.20	2.87
Average catch abundance (n) per fishing trip	13.95	5.36
Percentage biomass of top 10 spp (%)	77	81
Percentage abundance of top 10 spp (%)	81	47

The ordinations of CPUE by abundance and biomass showed that 30%–49% of the variation in CPUE was explained by LULC (Table 5, Figs. 3 and 4). These ordinations also showed a clear separation of the species that had the strongest relationships with habitat into forest-associated species (*Alestes macrophthalmus*, *Schilbe mystus*, *Synodontis decorus*, and *Brycinus macrolepidotus*) and those that appeared to thrive in the mixed forest and agriculture floodplain landscape (*Labeo macrostoma*, *Distichodus mossambicus*, *Labeo lukulae*, and *Synodontis greshoffi*). These relationships with LULC were in addition to any specific river morphology and substrate associations (Figs. 3 and 4), thereby revealing LULC effects on fish catch regardless of differences across rivers.

3.3. *Fish diet and condition*

We found some evidence that niche breadth of the diet of nine species together was higher in the Boumba (mean $= 0.32$) than in Kadey (mean $= 0.17$), although the niche breadth of six species was nearly identical and the significance of the t-tests was low (p-value $= 0.055$; see INB data in Table 6). Three species (*Synodontis decorus*, *Labeo macrostoma* and *Marcusenius mento*) had broader diet breadths in the forested Boumba River than in the Kadey River where agricultural landscape dominated. Four species (*Brycinus imberi*, *Campylomormyrus tamandua, Synodontis decorus* and *Synodontis pleurops*) had greater proportions of food items from terrestrial vegetation in the Kadey than in the Boumba.

We did not find evidence of differences in the occurrence of diseases and parasites in the specimens between the two rivers (Table 6). For most species, occurrence of DELT in the two rivers were similar, with the exception of *Brycinus imberi*, which exhibited a higher occurrence of deformities and lesions in the Kadey River (Table 6; $p = 0.13$).

4. Discussion

4.1. *Land-use land-cover effects on inland fish catch*

Our results indicate that LULC and in particular floodplain forests affect fish catch and provide preliminary evidence that such effects involve, among other factors, changes in fish diets. Contrary to expectations however, we did not find evidence that LULC affects fish health. Overall, our results are in line with the notion that floodplain forests support fish populations in rivers with relatively limited floodplain areas in ways similar to that of small streams or rivers with very large floodplains (e.g., Amazon). This suggests that resource use activities that incur the loss of floodplain forests such as agriculture and cattle ranching may adversely affect fish populations in all lotic ecosystems. Growing LULC trends in the tropics may thus affect fish catch more than previously anticipated. Depending on the scale with which these habitat losses occur, they can threaten the food, income, and livelihoods provided by inland fisheries.

Our finding that 30% of the variation in CPUE by abundance and biomass is explained by LULC demonstrates clear LULC controls on inland fish catch. At least two of the three broad categories of habitat

Table 4

Results of LASSO-regularized Poisson regressions indicating the regression coefficients (standardized) of variable retained for each of 16 species. A '.' Indicates that the variable was dropped from the model and is insignificant. Response variable was species abundance and candidate explanatory variables were habitat characteristics. Key to species: Labmac- *Labeo macrostoma*, Dismos- *Distichodus mossambicus*, Alemac- *Alestes macrophthalmus*, Schmys- *Schilbe mystus*, Labluk- *Labeo lukulae*, Syndec- *Synodontis decorus*, Brymac- *Brycinus macrolepidotus*, Syngre- *Synodontis greshoffi*, Petsim- *Petrocephalus simus*, Marmen- *Marcusenius mento*, Bryimb- *Brycinus imberi*, Dissex- *Distichodus sexfasciatus*, Baguba- *Bagrus ubangensis*, Camtam- *Campylomormyrus tamandua*, Disaff- *Distichodus affinis*, Synple- *Synodontis pleurops*.

Variable	labmac	Dismos	Alemac	Schmys	Labluk	Syndec	Brymac	Syngre	Petsim	Marmen	Bryimb	Dissex	Baguba	Camtam	Disaff	Synple
Intercept	−7.44	−1.93	−2.24	−2.35	−2.19	−1.08	−0.21	−3.09	−1.39	−2.09	−1.88	−2.52	−3.64	−2.73	−0.80	−1.19
Boumba	−0.37	.	2.54	1.92	.	.	0.55	.	.	.	.	.	.	.	.	.
Kadey	3.12	1.35	.	.	.	.	.	1.38	.	.	.	.	.	.	.	.
Aver. site width (m)	−0.01	.	−0.01	0.00	.	−0.01	−0.01	.	.	.	.	0.01	.	.	.	.
Max. site depth (m)	0.96	.	.	.	0.19	.	0.16	.	0.01	.	.	.	.	.	.	.
Aver. site depth (m)	0.66	0.38	0.69	0.62	.	.	.	0.27	.	0.03	0.11	.	.	.	.	.
Velocity (m/s)	−2.18	0.31	.	−0.22	.	.	.	.	.	.	.	.	.	.	.	.
Morphology (Run/Riffle = 1)	1.92	−0.28	−0.17	.	.	.	.	.	.	.	.	.	.	.	.	.
Substrate (Clay = 1)	−2.88	−1.56	.	−0.79	.	.	.	.	.	0.24	.	.	.	.	.	.
Substrate (Sand = 1)	−3.37	−1.72	−0.14	−0.74	0.23	−0.08	.	.	.	.	.	.	.	.	.	.
Substrate (Boulder = 1)	.	−0.38	.	.	−0.48	.	.	0.82	.	.	.	.	.	.	.	.
Floodplain LULC (Open Canopy = 1)	.	−0.73	.	.	0.46	.	.	.	.	.	.	.	.	.	.	.
Site LULC (Closed Forest = 1)	−0.73	.	0.09	.	−0.05	1.74	0.61	.	0.04	.	.	.	.	.	.	.
Gear Location (Midriver = 1)	0.44	.	1.20	0.13	.	0.27	.	0.36	−0.37	.	.	.	.	.	.	.

variables used in our models (i.e., LULC, substrate, and river morphology/velocity) were related to ten of the 16 species studied, with seven of the species being related to LULC in the floodplain areas. These findings are supported and in part explained by previous studies. The mostly positive relationships indicating forested areas generally host higher fish abundance and biomass, as floodplain forests are known to improve water quality, availability and stability of physical complex structures, and availability and diversity of food items for fish (Lo et al., 2020). Forested areas may also host higher fish abundance and biomass because fish often actively select for flooded floodplain forests in search for suitable habitat conditions (Castello, 2008; Castello et al., 2018).

Although most species abundances and biomasses tended to be positively related to LULC, species responses to LULC depended on species traits. Species associated with forests were diverse in their traits, comprising both medium- and large-bodied types (Fig. 2). The medium-bodied species were mostly laterally compressed, pelagic to whole water column dwellers, sight-feeders with prominent eyes, and either carnivores or omnivores. The large-bodied species were deep, pelagic (and from the same family; Alestidae) and generalist feeders as juveniles but exhibit ontogenetic diet shifts (juveniles eat weed, beetles, and other insects and adults eat mostly fish). These species preferred habitats with slow moving water; vegetated areas and floodplain, and open water, and are more likely to use habitats similar to those found within the Boumba River, which had a high proportion of pools. In comparison, the traits of species associated with mixed forest and agriculture were less diverse than those associated with forests, likely because disturbed environmental conditions filter out the diversity of traits and functional roles (Keck et al., 2014; Öckinger et al., 2010). Species associated with mixed forest and agriculture were mostly large-bodied, deep or laterally compressed in form; pelagic or benthopelagic; detritivores, herbivores or omnivores; and preferred habitats with relatively fast flowing water and open areas with vegetation (Fig. 2). Those species thrived better within the Kadey sites, which were wider, had faster flow and sandy or sand and boulder substrates. Similar patterns of filtering of species traits associated with loss of forests in our study has been observed elsewhere. In small streams from southern Brazil, grassy vegetation associated with agricultural fields was associated with increased redundancy of functional roles in the ecosystems (Casatti et al., 2015). In the large Amazon floodplains, deforested areas were associated with the replacement of species with unique combinations of functional traits with species that are ecological generalists with traits shared with other species (Arantes et al., 2018).

Our results provide some insights into the mechanisms by which LULC affect river fish assemblages. Forested areas provide fish with allochthonous organic materials, including C_3 plant parts (e.g., tree seeds, fruits, and leaves) and terrestrial invertebrates (Bojsen, 2005) that are key sources of carbon supporting fish biomass (Oliveira et al., 2006; Ou and Winemiller, 2016). In particular, forest leaf litter supports fish by increasing availability of key food items such as invertebrates (Giam et al., 2015). Deforestation of small streams has been shown to decrease this provision of forest (terrestrial) food items for fish while providing fish with greater abundance of autochthonous materials, including algae stemming from increased sunlight exposure (Bojsen, 2005). These habitat changes appear to favor species more reliant on autochthonous food items and adversely affect those more reliant on autochthonous food items (Bojsen, 2005). Those effects are thought to induce shifts in community structure through decreased diversity of trophic functions in sites affected by LULC change (Zeni and Casatti, 2014). Our results add to that body of knowledge by providing preliminary indication that fish benefit from greater diversity of food items in forested areas, and that species diets characterized by greater plasticity are more likely to adapt to mixed forest and agricultural areas, although based on a more restricted set of food items. Therefore, it would seem that LULC change affects fish assemblages in river floodplains not only by changing species composition, as documented previously (Arantes et al., 2018; Casatti et al., 2015), but also by changing the diets of individual species.

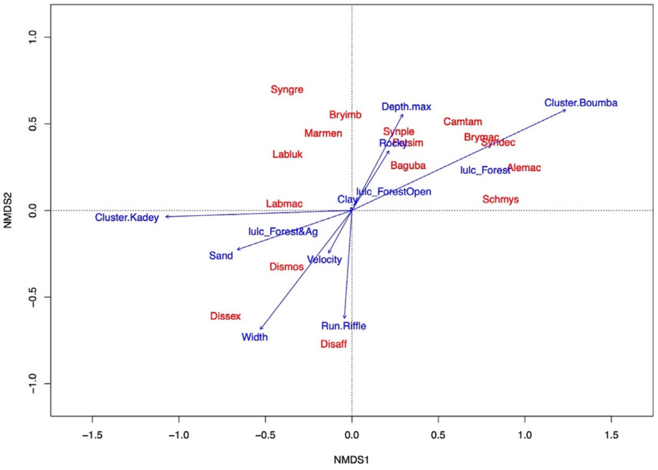

Fig. 3. Biplot of non-metric multidimensional scaling (NMDS) ordination of catch-per-unit-effort (CPUE) by abundance, showing the habitat associations of species that occurred in both the Boumba and Kadey rivers. Key to species: Labmac- *Labeo macrostoma*, Dismos- *Distichodus mossambicus*, Alemac- *Alestes macrophthalmus*, Schmys- *Schilbe mystus*, Labluk- *Labeo lukulae*, Syndec- *Synodontis decorus*, Brymac- *Brycinus macrolepidotus*, Syngre- *Synodontis greshoffi*, Petsim- *Petrocephalus simus*, Marmen- *Marcusenius mento*, Bryimb- *Brycinus imberi*, Dissex- *Distichodus sexfasciatus*, Baguba- *Bagrus ubangensis*, Camtam- *Campylomormyrus tamandua*, Disaff- *Distichodus affinis*, Synple- *Synodontis pleurops*.

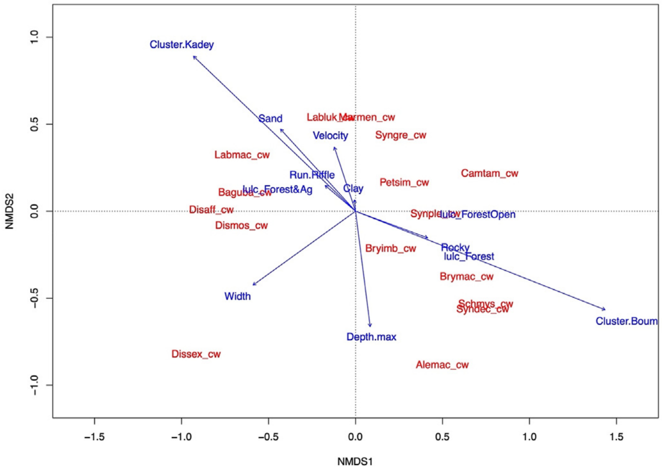

Fig. 4. Biplot of non-metric multidimensional scaling (NMDS) ordination of catch-per-unit-effort (CPUE) by biomass, showing the habitat associations of species that occurred in both the Boumba and Kadey rivers. Key to species: Labmac- *Labeo macrostoma*, Dismos- *Distichodus mossambicus*, Alemac- *Alestes macrophthalmus*, Schmys- *Schilbe mystus*, Labluk- *Labeo lukulae*, Syndec- *Synodontis decorus*, Brymac- *Brycinus macrolepidotus*, Syngre- *Synodontis greshoffi*, Petsim- *Petrocephalus simus*, Marmen- *Marcusenius mento*, Bryimb- *Brycinus imberi*, Dissex- *Distichodus sexfasciatus*, Baguba- *Bagrus ubangensis*, Camtam- *Campylomormyrus tamandua*, Disaff- *Distichodus affinis*, Synple- *Synodontis pleurops*.

Table 5

Relationship between habitat variables and vectors (axes) of non-metric multidimensional scaling (NMDS) ordination of catch-per-unit-effort (CPUE) based on abundance (upper) and biomass (lower) of fish caught.

	NMDS1	NMDS2	r^2	Pr(>t)
CPUE based on abundance				
River Cluster 1 - Boumba	0.9050	0.4254	0.49	0.0003 *
River Cluster 2 - Kadey	−0.9994	−0.0339	0.30	0.0053 *
Average Reach Width (m)	−0.6103	−0.7921	0.19	0.0462 *
Maximum Reach Depth (m)	0.4680	0.8837	0.10	0.2250
Velocity (m/s)	−0.4821	−0.8761	0.02	0.7584
Morphology (Run/Riffle = 1)	−0.0703	−0.9975	0.10	0.2263
Substrate (Clay = 1)	−0.3819	0.9242	0.00	0.9985
Substrate (Sand = 1)	−0.9461	−0.3239	0.12	0.1491
Substrate (Rock/Boulders = 1)	0.5286	0.8489	0.04	0.5557
LULC - Factor Centroids			0.30	0.0008*
Reach Closed Forest	0.7719	0.2319		
Reach Mixed Forest & Agriculture	−0.3970	−0.1263		
Floodplain Open Canopy	0.2426	0.1047		
CPUE based on biomass				
River Cluster 1 - Boumba	0.9300	−0.3676	0.51	0.0002 *
River Cluster 2 - Kadey	−0.7228	0.6911	0.36	0.0020 *
Average Reach Width (m)	−0.8110	−0.5850	0.11	0.1964
Maximum Reach Depth (m)	0.1258	−0.9921	0.09	0.2530
Flow Velocity (m/s)	−0.3145	0.9493	0.03	0.6252
Morphology (Run/Riffle = 1)	−0.7628	0.6466	0.01	0.8551
Substrate (Clay = 1)	−0.0944	0.9955	0.00	0.9879
Substrate (Sand = 1)	−0.6749	0.7379	0.08	0.2789
Substrate (Rock/Boulders = 1)	0.9378	−0.3471	0.04	0.5670
LULC - Factor Centroids			0.30	0.0004 *
Reach Closed Forest	0.6538	−0.2610		
Reach Mixed Forest & Agriculture	−0.4470	0.1209		
Floodplain Open Canopy	0.7038	−0.0219		

* denotes significant variables.

However, contrary to expectations, six of the nine species analyzed fed more heavily on terrestrial vegetation in the Kadey River where mixed forest and agricultural areas dominated, than in the Boumba River where forested areas dominated. Although such results are preliminary, we suggest they may be explained by increased erosion stemming from the agricultural lands of the Kadey River. In addition to providing leaf litter inputs, riparian forests tend to reduce soil erosion from adjacent agriculture (Dale Jones III et al., 1999). Consistent with this suggestion, water clarity in the Kadey River was more turbid than in the Boumba River, although our observational data do not allow us to know if that increased turbidity is natural or a result of LULC patterns.

These observed shifts in fish diets could be expected to lead to changes in fish health as measured by DELT. Studies in small streams have often found increased DELT prevalence in fishes inhabiting degraded areas with increased water turbidity (Schleiger, 2000). In particular, two studies showed that fish condition, as measured by the Fulton index (a measure of the plumpness of fish), varied both positively and negatively in small streams as a function of riparian forest presence (Bojsen, 2005; Vila-Gispert et al., 2000). However, our finding showing no differences in DELT for the same group of species in the Boumba and Kadey rivers suggests four possibilities (i) LULC did not affect fish condition or (ii) this lack of difference resulted from our small sample sizes. (iii) Plasticity in diet and habitat selection allowed fish to successfully adapt to both habitat types. (iv) Some combination of all these potential explanations occurred. Given the importance of fish health and condition to assessing potential habitat change effects on fish catch, further research on the topic is necessary.

4.2. *Consequences for food security*

The dependence of fish on LULC has key implications for food security. The five species whose abundance was positively related to forested sites (*Petrocephalus simus*, *Brycinus macrolepidotus*, *Synodontis decorus*, *Alestes macrophthalmus*, *Distichodus mossambicus*) comprised 22% and 24% of the catch in weight in the Kadey and Boumba rivers, respectively. In comparison, the two species whose abundance was negatively related to forested sites (*Labeo lukula* and *Labeo macrostoma*) comprised only 4% of the catch in weight in both rivers. Although our results do not quantify the extent to which fish catch is lost as a function of deforestation, they are consistent with two previous analyses that showed that multispecies fish catch decreased with losses of floodplain forests (Barros et al., 2020; Castello et al., 2018). Such losses in fish catch may not seem large, but

Table 6
Comparison of fish diet indicators and fish condition in the Boumba and Kadey rivers. For nine taxa that were caught in both rivers, the table shows the values of the index of diet niche breadth (INB) and the relative contribution in weight of terrestrial vegetation. Variance estimates (Stand. Dev.) are shown in parenthesis. The relative occurrence of DELT (i.e., deformities, eroded fins, lesions and tumors) for each of the nine fish species caught in both rivers is shown. *P*-values of the chi-square tests of DELT values for all species across rivers are shown in parenthesis.

Species	Niche breadth (INB)		Terrestrial veget. (%)		DELT (%)			Sample Size (*n*)	
	Boumba	Kadey	Boumba	Kadey	Boumba	Kadey	(*p*-value)	Boumba	Kadey
Brycinus imberi	0.22	0.18	0.05 (0.04)	0.19 (0.18)	0.2	0.64	(0.13)	5	14
Brycinus macrolepidotus	0.18	0.17	0.32 (0.44)	0.2 (0.35)	0.47	0.51	(0.83)	34	30
Campylomormyrus tamandua	0.14	0.17	0.21 (0.18)	0.66 (0.33)	0.11	0	(1)	9	4
Distichodus mossambicus	0.002	0.09	0	0	0.2	0.05	(1)	5	17
Labeo macrostoma	0.47	0.005	0.05 (0.05)	0	0.26	0.24	(1)	23	9
Marcusenius mento	0.51	0.25	0	0	0	0	–	5	5
Schilbe mystus	0.25	0.26	0.12 (0.09)	0.09 (0.07)	0	0	–	30	22
Synodontis decorus	0.7	0.11	0.21 (0.18)	0.66 (0.33)	0	0	–	6	3
Synodontis pleurops	0.4	0.35	0	0.44 (0.27)	0	0	–	3	9

they should not be disregarded even if they are somehow compensated by increased availability of other food items, particularly because of the well-known health benefits of fish for diets (Willet et al. 2019; Thilsted et al. 2016). The rapid rates with which food demand has been increasing in tropical developing nations, combined with growing impacts on river populations and ecosystems (e.g., by pollution, overfishing, and dam construction) can make even small losses in fisheries problematic for the people who depend on them. Riverine people often adapt to such environmental changes by increasing consumption of alternative animal protein sources (e.g., chicken) or processed food items (e.g., canned meat; Isaac et al., 2015) that typically lack the nutritional value of wild caught fish (Kawarazuka and Béné, 2011). Dietary intake data collected from women of reproductive age in communities living around the Kadey ($n = 496$) and Boumba ($n = 500$) rivers as part of a parallel study in this project show the importance of fish in diets, particularly around the Kadey. Fish comprised 61.9% of animal source foods consumed by women averaged across dry and rainy seasons in the Kadey communities and about 33% of animal source foods for women living near the Boumba River. For those who consumed fish, wild caught local fish contributed 23% of the protein, 18% of calcium, and 16% of the vitamin B12 consumed in the Kadey site. In the Boumba site, wild caught local fish contributed 10% of the protein, 12% of the calcium and 32% of the vitamin B12 consumed.

4.3. Policy implications

The adverse effects of LULC change on inland fish catch and food security can be minimized and even prevented through policies that require the maintenance of native vegetation in riparian and floodplain areas. A key challenge, however, is that freshwater ecosystems worldwide and particularly in the tropics suffer from much less protection compared to their terrestrial counterparts (Leal et al., 2020). The few policies that exist for freshwater ecosystems are usually protections to stream or river riparian buffers, which can vary in width depending on the nation and the width of stream or river channels, and thus may not provide sufficient protection. An additional challenge is that, even when such riparian protection policies exist, compliance often is poor, as tropical nations tend to have limited human and financial resources to enforce them adequately (Barlow et al., 2018). In Peru, for example, the average protected riparian buffer is only about half the legally required width (McClain and Cossio, 2003).

While many nations have such riparian protection policies, provisions included in Cameroon's Forest Law of 1994 appear to be ‘optional’ in that they apply only in cases where they are deemed necessary. Specifically, Section 17 of that Forest Law states: “*if the creation or maintenance of permanent forest cover is considered necessary for soil preservation, protection of the banks of a stream or of a river, regulating water flow or preserving biodiversity, the surrounding land may either be declared out of bounds or as an ecologically fragile area, or classified as protected State forest, full nature reserve, or wildlife sanctuary as the case may be, under conditions laid down by decree.*" Our results indicating that loss of forest cover is associated with decreased inland fish catch for local people of the Kadey and Boumba rivers could underpin the rationale for requiring the protection of riparian and floodplain forests.

5. Conclusions

In sum, we found evidence that LULC affects fish catch mainly through changes in the extent of floodplain forests of medium-sized rivers. Such effects appear to involve fish diets and instream habitat features (i.e., riparian canopy closure, water clarity, substrate heterogeneity, and habitat volume), but not fish condition in terms of diseases or deformities, eroded fins, lesions or tumors. These LULC effects on fish populations imply that prevailing trends in LULC around the world threaten the food and livelihood security associated with inland fisheries. They highlight the importance of well-designed policies to maintain native vegetation along riverbanks and in floodplain areas.

Ethic statement

This study was exempted from need to have an ethics committee approval. All information collected from fishers was collected only after they explicitly provided their consent (as detailed in the main text).

Conflict of interest

The authors declare no financial, competing, or conflict of interest.

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Authors' contribution

Leandro Castello: Conceptualization, Methodology, Writing- Original draft preparation; Emmanuel Frimpong: Conceptualization, Methodology; Writing - Review Editing; Gifty Anane-Taabeah Attu, Anthony Aliebe, Nelly Ornell Onana Ateba, Sandrine Jueya: Investigation, Writing - Review & Editing; Felipe Carvalho; Investigation, Writing - Review & Editing; Amy Ickowitz: Funding acquisition, Writing - Review & Editing.

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