

Human and environmental influences on the distribution and abundance of arapaima in river  
floodplains of the Lower Amazon

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ABSTRACT (Academic)

Understanding the factors influencing the abundance and distribution of tropical floodplain fishes is an important component of fisheries management plans to support future sustainable resource use. This thesis uses a multi-scale approach to understand the habitat factors controlling the distribution and abundance of arapaima (*Arapaima spp.*) in river floodplains of the lower Amazon River, near the municipality of Santarém, Pará State, Brazil. In chapter 1, a study of eight environmental variables in 13 dry season floodplain lakes demonstrates that lake depth, relative depth, conductivity, and transparency were significantly related to the probability of arapaima presence at individual locations within lakes. Further, the study revealed that smaller arapaima were more likely to be found near macrophyte coverage than in open water locations. In chapter 2, a landscape scale approach was used to examine the interactions between management systems, landscape habitat coverage, and spatial arrangement on arapaima population sizes in 73 floodplain lakes. Results showed that all three influences were important in explaining variability in arapaima abundances. Management and habitat variables contributed equally in controlling arapaima abundances. Both had strong patterns of spatial arrangement and overlapped significantly, suggesting that analysis of either management systems or landscape habitats without the other would lead to overestimations of the strength of their influence. Findings from both chapters support the notion that future sustainable use of arapaima populations requires a dualistic approach combining habitat conservation with fisheries management techniques enacted at a local scale.

## ABSTRACT (Public)

Understanding where fishes choose to live within aquatic habitats, and why they do so, is important for their long-term protection habitat destruction and overfishing. This thesis looks at fish habitats at both small and large scales to understand the variables affecting populations of the megafish arapaima (*Arapaima spp.*) in lakes of the lower Amazon River, near the municipality of Santarém, Pará State, Brazil. In chapter 1, a study of eight environmental variables in 13 lakes shows that for each lake, deeper, muddier (less clear), and more electrically-conductive waters were more likely placed to find arapaima. Further, the study revealed that young arapaima were more likely to be found near aquatic plants than in open water areas near the middle of the lake. In chapter 2, a larger-scale approach was used to examine the interactions between humans, habitats, and spatial groupings for arapaima population sizes in 73 lakes. Results showed that all three factors were important in explaining how many arapaima were found in each lake. Human and habitat variables were equally important variables affecting arapaima. Both were strongly related to spatial groupings and overlapped significantly, suggesting that analysis of either human systems or habitats without the other would lead researchers to overestimate how important they are for arapaima. Findings from both chapters support the notion that future sustainable use of arapaima populations requires an approach combining habitat conservation with fisheries management techniques enacted at a local scale.

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## **Preface**

The study of fish that have significant value to humans has long comprised two primary schools of inquiry: ecologists who study the fish in their natural environment, and social scientists who study management and human uses of fish. As the increasing needs of a growing human population continually pressure the world's natural resources, better understanding and management is needed. Ensuring the long-term sustainability of fisheries resources will require collaborative approaches that unite scientists across disciplines to develop comprehensive methods for understanding and solving problems. This thesis applies an interdisciplinary approach to determine the human and environmental factors influencing the distribution and abundance of arapaima (*Arapaima* spp.) in the Lower Amazon River, near the municipality of Santarém, Pará State, Brazil.

Both chapters of this thesis focus on arapaima populations in the nutrient-rich, whitewater-influenced habitats of the lower Amazon River near Santarém. These floodplain areas, collectively known as várzea, contain forests, grasslands, lakes, streams, and river channels that continually shift as erosion and sedimentation shape the landscape (Junk, 1997). Fish richness and abundance in Amazon River floodplains are strongly related to flooded forest areas and proximity river channels (Lobón-Cerviá *et al.*, 2015). Regular and predictable seasonal changes in floodplain fish assemblages are known to occur as a result of the flood-pulse cycle (Rodríguez and Lewis, 1994). Seasonal flooding of forest areas adjacent to floodplain lakes connects large areas, which allows fish to take advantage of expanding food and habitat resources (Galacatos *et al.*, 2004). A number of fish species in Amazon floodplains undergo lateral migrations related to breeding and physical habitat changes throughout the flood cycle (Fernandes, 1997; Castello, 2008a).

The seasonal replenishing of nutrients (Melack and Forsberg, 2001), stable tropical temperature regime, and immense productivity (Goulding, 1999) of the várzea systems in the lower Amazon have made them ideal locations for human inhabitants. The abundance of natural resources, coupled with the ease of transportation afforded by the large-river system, make the várzea vulnerable to exploitation – particularly of fish populations – from a multitude of sources. As the human population within the area grows, deforestation to support agriculture in the nutrient-rich várzea soils is an increasing problem (Neill *et al.*, 2001). Historically, fishing has served as a vital source of sustenance and income for a significant portion of the native human population (Crampton *et al.*, 2004). Fish species diversity in the Amazon River basin is extraordinary, with >2,500 described species (Val and Almeida-Val, 1995; Reis *et al.*, 2003) and estimates of >1,000 undescribed species. However, only ~700 fish species exist in the várzea ecosystem, and of these less than ten species comprise over three-quarters of the commercially-harvested fish biomass (Crampton *et al.*, 2004). As a result, many fish species vital to the local economy have been overexploited to the point of localized extinctions, prompting a need for conservation efforts. Among these species is the arapaima – one of the fishes of greatest conservation concern in the lower Amazon (Castello and Stewart, 2010).

The arapaima is a large-bodied (up to 3 m) member of the Osteoglossiformes with unique adaptations to the Amazon floodplain ecosystem. Commonly achieving sizes >65cm (Arantes *et al.*, 2010) within the first year of life, their modified swim bladder makes them obligate-air breathers; an adaptation which makes them uniquely suited to the harsh conditions within várzea lakes during the dry season. Arapaima build nests for spawning when the waters begin to rise at the beginning of the flood season. The young-of-year fish then hatch shortly before the floods reconnect the entire várzea ecosystem, at which point males escort their young through the

flooded forest to forage for approximately three months (Queiroz, 2000; Castello, 2008b). Recent studies (Stewart, 2013a, 2013b) have suggested that the species *Arapaima gigas*, which has traditionally been the only recognized species of the *Arapaima* family, may actually comprise several distinct species. To date, studies have not conclusively demonstrated differences and range descriptions for the proposed splitting of *Arapaima gigas* into multiple species, thus this thesis will assess arapaima as a unified group. Whereas the arapaima's air-breathing makes it a particularly efficient predator within the extreme conditions of the várzea, it also leaves the fish uniquely susceptible to overfishing. Because it must surface every 10-15 minutes for air (Goulding *et al.*, 1996; Queiroz and Sardinha, 1999), the arapaima can easily be tracked and hunted by local fishermen. Their fast growth, prized meat, and ease of capture have resulted in arapaima populations throughout the Amazon becoming threatened or locally-extirpated (Castello *et al.*, 2015a). However, the arapaima is not unique in regards to overfishing. A number of other fish species that utilize the floodplain lake and seasonally-flooded forest habitats face strong fishing pressures that threaten the long-term sustainability of their populations (Goulding, 1999; Crampton *et al.*, 2004; Isaac and Ruffino, 2007).

Understanding and managing the threats to arapaima (and other fish) populations necessitates interdisciplinary knowledge that is greater than the sum of individual disciplinary components. However, putting all of the parts together has traditionally been a challenge. Considering ecological and anthropogenic phenomena in isolated contexts rather than as dynamic, interacting factors hampers the ability to predict outcomes for important systems (Bozelli *et al.*, 2009), such as arapaima population management. Integration of both human and environmental influences (Agrawal, 2001) in models describing fish abundances and distributions is a critical step in developing effective conservation schemes. In order to

understand these systems, scientists have developed frameworks, such as the social-ecological systems (SES) model (Ostrom, 2009), which link humans, management, natural resources, and ecosystems together in unified models. By simultaneously considering all of the components interacting within these systems, researchers hope to understand the factors contributing to – or detracting from – the sustainable use of these systems. While these models provide excellent foundations for interdisciplinary assessment of sustainability, to date, their use has been largely biased in favor of the social science aspects of the models (Epstein *et al.*, 2013; Vogt *et al.*, 2015). Meanwhile, ecologists have continued to operate largely within their own discipline while ignoring the human influences to their target species or ecosystem. However, I do not intend to discount the merit of disciplinary research. On the contrary, I believe that true interdisciplinary research will require more single-disciplinary rigor than ever before. Each successive contribution granted by a single disciplinary study is like a piece added to a puzzle; we cannot solve the puzzle without first holding the necessary pieces. The difficulty lies in assembling the disparate pieces into a unified picture of the system as a whole.

Nowhere is the need for building such detailed interdisciplinary approaches more apparent than the Amazon River basin, where the rapidly developing human population is increasingly linked to the outside world through the harvest of the Amazon's bountiful natural resources. In this thesis, I address the challenges of understanding and managing arapaima fisheries in floodplains of the Lower Amazon River. I do so in the spirit of focusing my abilities to contribute to a larger body of knowledge for arapaima, and indeed fisheries management as a whole. Whereas previous studies had identified patterns of habitat selection among various floodplain lakes during the dry season (Tejerina-Garro *et al.*, 1998; Arantes *et al.*, 2013), in chapter 1 I conduct an assessment of the habitat factors affecting the distribution of arapaima

*within* lakes during the dry season. This work investigates the importance of several key floodplain lake habitat variables on the distribution of arapaima individuals at distinct periods of their life cycles. In chapter 2, I contribute to the science of SES research by conducting an integrated assessment using a series of datasets on arapaima abundances, landscape habitat classifications, and human governance of arapaima fisheries by using spatial analysis as a linking mechanism between multiple disciplines. The purpose of this analysis is to address the largely unexplored question of estimating relative importance of human versus environmental influences that control the abundance of fish populations.

Fish ecology in the Amazon and assessments of tropical fisheries are both largely unexplored frontiers. It is my hope that this thesis will constitute a small, but potentially useful, piece to each of these puzzles. Just as this research was built upon (and in collaboration with) the work of others, I aim to contribute something meaningful to the next person seeking to push the science of sustainability forward by another small step.

**Chapter 1.** Size-structured habitat selection by arapaima in dry season Amazonian floodplain lakes

**Abstract**

Identifying habitat selection patterns throughout the lifespan of river floodplain fishes is important for identifying areas of conservation interest. However, few studies have attempted to characterize the extent to which intra-lake variables influence habitat selection at multiple life-stages for tropical floodplain fishes in dry-season floodplain lakes. The goal of this study was to examine the effects of environmental factors (i.e., depth, water chemistry, refugia) on habitat selection patterns by arapaima *Arapaima* spp. and determine the extent to which these relationships differ across three distinct size classes. In 13 floodplain lakes of the lower Amazon River, variables were measured at locations representing habitat availability and compared to measurements taken where arapaima were observed during surface-breathing. Generalized linear mixed models (GLMM) were used to account for variability from human effects in different lakes and probability of arapaima presence at each sample location was modeled based on the variables measured. Arapaima expressed distinct habitat selection patterns and significant differences across size classes. The general pattern observed was that all arapaima were more likely to be found in deeper, more turbid, and higher-conductivity locations, while smaller arapaima were more likely to remain near areas of dense floating macrophytes. The probability of arapaima presence differed significantly among fishing community territories, reflecting differences in fishery management. This study reveals that depth, water clarity, and macrophyte cover can govern patterns of habitat selection in floodplain fishes during the dry season and suggests patterns of current habitat destruction for agriculture may disrupt important habitats for fishes.

## **Introduction**

Tropical river floodplain ecosystems are among the most important locations to human populations in developing regions (Junk, 2002; Tockner and Stanford, 2002), as they make excellent grounds for fisheries, settlements, and agriculture while also providing a means of transportation. Rapid development of these areas has resulted in significant deforestation (Renó *et al.*, 2011) and depletion of tropical fisheries (Castello *et al.*, 2013) crucial to the income- and food-security of some of the world's poorest populations (Coomes *et al.*, 2010; Ziv *et al.*, 2012). Balancing human development with conservation to ensure the continued productivity of floodplain fisheries requires knowledge of which habitats are most important in supporting heavily-exploited fishes. During the dry season, floodplain fishes are often concentrated into small lakes (Winemiller and Jepsen, 1998), making them more susceptible to natural and human-induced mortality (Junk, 1984; de Yuan and de Hassan, 1985; Winemiller and Jepsen, 1998). Therefore, identifying the dry-season habitat factors important to floodplain fishes is an important step in determining locations for habitat protection. However, understanding of fish habitat selection in dry season lakes is limited, as most studies of floodplain fishes in dry season have historically focused largely on describing patterns of fish community structure. Further, many fishes exhibit changes in habitat selection as they grow (Schlosser, 1987; Lecchini *et al.*, 2007), but the extent to which this pattern applies to tropical floodplain fishes is largely unexplored. Developing effective conservation strategies for tropical floodplain fishes will likely necessitate protection of key habitats supporting fish. Understanding dry season intra-lake habitat selection at various life stages is an important step in identifying key habitats for protection.

Floodplain fish distribution and habitat selection are driven primarily by the effects of the flood pulse, a yearly cycle fluctuating between the high water levels of the flood season and the

relative scarcity of aquatic habitats during the dry season (Junk *et al.*, 1989). Following the lowest water levels of the year, rising waters create a moving littoral zone that advances from low water habitats into adjacent areas until the entire floodplain becomes a single connected aquatic habitat that includes river channels, floodplain lakes, macrophyte beds, and flooded forests. As waters recede, the littoral zone retreats until main river channels and floodplain lakes are the only aquatic habitats available. Many fishes migrate laterally during high waters to forage and seek cover in vegetated floodplain habitats (Fernandes, 1997; Castello, 2008a). When water levels recede, these fishes migrate back to main river channels or dry-season floodplain lakes in search of refugia from habitat reductions, where they must tolerate poor water quality characterized by high temperature, low pH, and low dissolved oxygen levels (Welcomme, 1979; Magoulick and Kobza, 2003). Within dry-season lakes, limited habitat availability increases fish density (Matthews, 1998; Magoulick and Kobza, 2003; Matthews and Marsh-Matthews, 2003), and consequently intensifies biotic interactions (Welcomme, 1979; Schlosser *et al.*, 2000). These concentration effects, induced by low water in river channels and floodplain lakes, make large-bodied, commercially-valuable species more vulnerable to fishing gear and overharvesting (Welcomme, 1995). Fish are known to migrate laterally between the highly productive floodplain habitats available during the flood season and the relatively restricted lake habitats of the dry season. While these movements likely reflect resource tracking in the flood season and selection of deep lakes promoting survival from desiccation in the dry season, little is known about the factors determining fish distribution and habitat selection within these dry season lakes.

In addition to changes following the seasonal influence of the flood pulse, floodplain fish habitat selection within dry season lakes can be expected to change as fish grow. Many fish species demonstrate distinct patterns of shifting spatio-temporal distributions across their

lifespans (Schlosser, 1987; Harvey and Stewart, 1991; Lecchini *et al.*, 2007). These changes in habitat selection influence survival rates by altering exposure to stressors that differentially influence individuals throughout their ontogeny. Early life stages are frequently more susceptible than adults to predation, and more sensitive to chemical and physical stressors (Kurihara, 2008; Baumann *et al.*, 2011). For younger or smaller individuals, risk of predation and foraging profitability are important drivers of habitat selection (Werner *et al.*, 1983; Werner and Gilliam, 1984; Mittelbach, 1986) that may shift as individuals grow to larger sizes. In tropical floodplains, where dry season lakes feature stressful water quality conditions and high predator concentrations, differentiation of habitat selection across the lifespan may be a key determinant of survival and recruitment. However, the role of habitat selection within dry-season habitats, and the extent to which it varies through ontogeny, is largely unknown. For tropical floodplain fishes, little is known about how habitat use across the lifespan influences species occurrence and vulnerability (Kouamé *et al.*, 2008), and most studies have focused on patterns of fish community structure rather than individual species or life stages.

Among threatened tropical floodplain fishes, arapaima (*Arapaima spp.*) are one of the largest and most historically important fish to Amazonian river-floodplain fisheries (Verissimo, 1895). They are of great conservation concern (Castello and Stewart, 2010), and in many areas, arapaima populations are being overexploited and depleted to the point of causing local extinctions (Castello *et al.*, 2015a). Arapaima are fast-growing, obligate air breathers that must gulp atmospheric oxygen from the water's surface or risk drowning. Their rapid growth to large sizes makes them strong candidates for investigating size-structured habitat selection. At birth, arapaima are only a few cm total length (TL), but they grow to ~ 1 m within the first two years of life. Arapaima reach sexual maturity at ~ 157 - 164 cm TL between three and five years of age,

and grow to an estimative maximum of ~ 3 m TL (Arantes *et al.*, 2010). Arapaima are generally found in slow-moving waters near the moving littoral edge (Castello, 2008a) and spawn during rising waters, when they build nests on forest margins in lake and connecting channel habitats (Castello, 2008b). During the flooded season, arapaima migrate laterally out of floodplain lakes and move between a variety of seasonally-available habitats (Castello, 2008a). They select the higher-elevation floodplain habitats (primarily flooded forests) when accessible during high waters and migrate back to the lower-lying floodplain lakes only when declining waters dry vegetated floodplain habitats (Castello, 2008a). While arapaima abundances in dry-season lakes of the central Amazon were positively correlated with lake depth, area, and conductivity (Arantes *et al.*, 2013), habitat selection by arapaima was not studied within dry-season lakes. Intra-lake variation in factors controlling the abundance of other floodplain fishes, such as dissolved oxygen, transparency, and macrophyte cover (Petry *et al.*, 2003a, 2003b), may also be important for arapaima. Previous studies documenting arapaima distribution have ignored the role of size-structured habitat selectivity, having assessed only individuals > 1 m TL (Arantes *et al.*, 2013). Understanding the habitat factors affecting arapaima distribution in dry-season lakes throughout their lifespan is an important step in designating habitats in need of protection under conservation schemes.

The purpose of this study was to (1) determine the factors influencing arapaima habitat selection within dry-season floodplain lakes and (2) evaluate how dry-season habitat selection of arapaima varies across life-stages.

## **Methods**

This study assessed arapaima habitat selection in 13 dry-season floodplain lakes by visually observing their presence at the moment of their obligate aerial breathing. To assess the extent to which habitat selection differed across the lifespan, individuals were classified into one of three life stages for comparison. Habitat variables were compared between locations where arapaima were present and systematically-sampled locations that represented available habitat types in each lake. Habitat variables were “spatialized” to account for spatial autocorrelation. A generalized linear mixed model (GLMM) was used to identify predictors of arapaima presence. An information theoretic (IT) approach was used to identify variable importance, and habitat use was compared across three size classes of arapaima.

### *Study Area*

The study area was the Amazon River floodplain near the municipality of Santarém, Pará, Brazil – an area of high concern for arapaima due to marked reductions in their abundance. The river channels and associated floodplains span more than 50 km in width during the dry season and encompass hundreds of fishing communities (Figure 1.1). Habitat alteration is prevalent throughout the region, with 56% of the floodplain deforested between 1970 and 2008 (Renó *et al.*, 2011). During the dry season, most floodplain lakes in the region are isolated from other water bodies. They vary in size from small ponds (one hectare) to large lakes (> 10 km in diameter).

During the dry season, most lakes are relatively shallow (< 3 m), hot (temperature > 30°), and turbid (secchi depth < 1 m), though the heterogeneity of the várzea creates distinct habitat patches within each lake. The lakes sampled were typically elliptical, with a series of concentric nested habitats within them (Figure 1.2). In most cases, a large central body of open water was surrounded by floating macrophyte beds 10-100 m wide, which were bordered by either dry

seasonally-flooded forests, cattle-ranching grounds, or dense “aningal” thickets (Figure 1.2). Aningal habitats are characterized by stands of *Montrichardia arborescens* mixed with floodplain trees so densely concentrated that they prevented entry for habitat sampling. The sample lakes were characterized by different habitat conditions, fishing pressures, and management regimes. Fishing rules and restrictions varied among communities, and among lakes within communities; multiple lakes from several communities were sampled to examine variability across environmental gradients and to account for differences in management practices. The extent to which arapaima populations among lakes interact when connected by flood waters is undescribed.

### *Sampling*

In order to determine what factors influence arapaima habitat selection, habitat variables were compared between collective locations where arapaima were present and other systematically-sampled locations representing the available habitat types in each lake. Lakes were surveyed between 12 November 2014 and 20 December 2014 from a canoe by one of us (J.C.R.) and a local expert fisherman paddling the perimeter of each lake near the open-water/macrophyte edge and across transects through the open-water areas (Figure 1.2). To assess habitat availability, eight habitat variables were measured at regular intervals around the perimeter and along the open-water transects. These intervals ranged 75 – 125 m and were determined for each lake such that habitat sampling could be accomplished in a single day. A paired sampling design was used near edge areas to quantify potential differences in habitat selection between open water and vegetated habitats for a given location. Measurements were

taken 10 m inside the macrophyte bed from the edge and 10 m in the opposite direction toward the open water.

To assess habitat use, measurements were taken at the exact locations where arapaima were observed surfacing to breathe. Arapaima presences were assessed by experienced fishermen, who were trained in a visual census method for arapaima (Castello 2004) that yields fish counts highly correlated ( $r = 0.983$ ) with mark-recapture estimates of the same populations. Arapaima were grouped into three size classes: ‘small’ (< 1 m TL), ‘medium’ (1-1.5 m TL), and ‘large’ (> 1.5 m TL). Based on available information (Arantes *et al.*, 2010), the small size class represents exclusively young fish (< 2 years old), the medium size class represents mostly juvenile fish (2-5 years old), and the large size class represents mostly adult fish (> 5 years old).

At each sampled location, a water quality meter (YSI 556 MPS) was placed just below the surface to measure temperature (°C), dissolved oxygen (DO, mg/L), conductivity ( $\mu\text{S}/\text{cm}^2$ ), and pH. A Hawkeye H22PX sonar depth sounder was used to measure depth. For open-water locations, a Secchi disk was used to measure water clarity, and a Nikon Prostaff rangefinder was used to determine distance from the nearest habitat patch providing cover (i.e., macrophyte beds or aningal habitats). Relative depth was estimated at each location to determine if individuals utilized the deepest areas available within lakes. Relative depth was calculated by dividing the measured depth at each location by the maximum depth observed within the lake. Because secchi depth cannot be measured under floating macrophyte beds without disturbing sediments, a nearest-neighbor approach (i.e., measurement at the closest location not obscured by macrophytes) was utilized for secchi depth in macrophyte locations in order to avoid issues arising from missing values in the analysis.

### *Data Analysis*

Many ecological analyses can be confounded by spatial autocorrelation among sites due to unquantified underlying spatial gradients. In order to avoid potentially spurious findings caused by spatial autocorrelation, habitat variables were “spatialized” prior to analysis; this approach allows researchers to account for spatial autocorrelation without sacrificing degrees of freedom in subsequent models due to the need to include separate spatial variables (Brind’Amour *et al.*, 2005; F. Dormann *et al.*, 2007). First, a pairwise Euclidean distance matrix of sampling location coordinates (latitude and longitude) was calculated using the *spDistsNI* function in the *sp* package (Pebesma and Bivand, 2005; Bivand *et al.*, 2013) in R (R Core Team, 2014). The distance matrix was then subjected to a principal coordinates of neighborhood matrices (PCNM) analysis using the *PCNM* function from the *PCNM* package (Legendre *et al.*, 2013) of R. This procedure identifies significant gradients in spatial clustering of sampling locations by testing for significance on Moran’s *I* of spatial autocorrelation of eigenvectors ( $\alpha = 0.05$ ). Next, all significant spatial eigenvectors with positive eigenvalues produced by the PCNM analysis were retained and used as potential independent variables in linear regression models to predict each habitat variable. The optimal model for each habitat variable was identified based on the lowest value of Akaike’s information criterion (AIC) using the *stepAIC* function in the *MASS* package of R. Finally, subsequent regression models for each variable were created using only the spatial predictors from the optimal model for each habitat variable. Predicted values from these models represent both spatial gradients and habitat characteristics, and were retained as factors predicting arapaima presence. Spatialized habitat variables were scaled and centered to mean = 0 and variance = 1 prior to analysis.

In order to determine the factors influencing arapaima habitat selection across all size-classes, a generalized linear mixed model (GLMM) predicting the probability of arapaima

presence based on habitat variables was developed. Habitat variables were pre-screened for multicollinearity using Pearson correlation indices in which  $|r| > 0.7$  indicated an unacceptably high correlation. A GLMM using the *glmer* function in the *lme4* package of R was used to estimate the effects of habitat variables and fishing community on arapaima. Depth, relative depth, temperature, conductivity, pH, dissolved oxygen, transparency, and distance from nearest cover were included as fixed effects in the model. To separate the habitat variables affecting arapaima habitat selection from other confounding influences, one fixed and one random effect were added to the model. Fishing community identity (hereafter, “community”) was included as a fixed effect to account for the relative influence of management rules on habitat parameters. A random effect of habitat measurement location nested within lake identity was included as a categorical variable to account for inherent inter-lake variability in habitat variables.

Use of GLMM models was necessary to model the habitat variables while accounting for confounding effects. However, individual GLMM models cannot estimate the relative importance of individual significant independent variables. Therefore, an information-theoretic approach was used to estimate the relative importance of each habitat variable in predicting arapaima presence. The *dredge* function in the *MuMin* package in R was used to calculate Akaike weights ( $w_i$ ) for GLMMs of all possible combinations of independent variables, including an intercept-only model. For each variable,  $w_i$  was summed for all models containing that variable. Variables with higher summed  $w$  values are considered more important (Burnham and Anderson, 2010).

Size-structured habitat selection was assessed using linear mixed models (LMMs) to evaluate differences in environmental variables across three size classes of arapaima. Because the goal of this study was to assess differences in habitat selection across size classes, lake

identity was specified as a random effect (rather than a fixed effect) in LMMs to make inferences generalizable across Amazon floodplain lakes. Individual fish located in floating macrophytes were excluded from the LMM assessing differences in distance from nearest cover by size class, as all individuals located in cover areas were recorded as a '0' for the nearest-distance metric. Tukey's Honest Significant Difference (HSD) was used to create pairwise comparisons between size classes for each habitat variable. All statistical effects were interpreted as significant at  $\alpha < 0.05$ .

## Results

Arapaima exhibited strong habitat selection with respect to lake and anthropogenic factors (Figure 1.3). Models predicting the probability of arapaima presence, based on 243 observed breathing events, indicated that arapaima presence was significantly affected by community, depth, relative depth, and transparency (Table 1.2). Arapaima were observed in similar frequencies across size-classes ( $n = 85$  small, 76 medium, 82 large) and were more likely to occur in deeper, more turbid areas. Arapaima presence was strongly influenced by the community associated with the lake. GLMM-predicted mean probabilities of occurrence ranged from  $0.80 \pm 0.02$  for Santa Maria to  $0.24 \pm 0.02$  for Tapara-Miri, and differed significantly among communities surveyed (Table 1.2). Santa Maria had the highest community-level mean probability of occurrence, while all other communities were significantly lower. Both relative depth and absolute depth had significant positive effects on probability of arapaima presence ( $p < 0.001$ ,  $p = 0.013$ , respectively), while transparency had a significant negative effect ( $p = 0.028$ ). Conductivity was strongly and positively related to arapaima presence ( $p = 0.0503$ ). Water temperature was consistently included in heavily-weighted models, but was not a statistically significant predictor of arapaima presence. Dissolved oxygen, pH, and distance from cover did

not significantly affect arapaima presence. The most important variable predicting arapaima presence was community ( $w = 1.0$ ), followed by relative depth ( $w = 0.99$ ), absolute depth ( $w = 0.93$ ), temperature ( $w = 0.91$ ) and secchi depth ( $w = 0.85$ ) – all of which were significant except for temperature (Figure 1.4). Other variables were relatively less important (see Table 1.1).

Models of habitat selection by individual size-classes showed that arapaima exhibited distinct patterns of size-structured habitat use (Figure 1.5). After accounting for differences among lakes, distance of fish from nearest cover differed significantly among size classes. For arapaima found in open water, small individuals were located significantly closer to floating macrophyte beds (distance =  $12.96 \pm 15.77$  m) than medium ( $29.07 \pm 22.81$  m) and large ( $30.33 \pm 21.60$  m) individuals (Table 1.3). Arapaima were found in open water habitats nearly twice as often as in cover habitats, and habitat type did not differ significantly among size classes (Chi-Square  $p$ -value = 0.38). Though depth appeared to differ between small arapaima ( $1.38 \pm 0.06$  m) and the two larger size classes (medium =  $2.25 \pm 0.21$ , large =  $1.73 \pm 0.14$ ), the difference was not significant when the random effect of lake was included. All other pairwise comparisons of environmental variables by size-class were insignificant.

## **Discussion**

The distribution of arapaima within dry-season lakes of the Lower Amazon was primarily influenced by the community in which lakes were located, depth, relative depth, conductivity, and water transparency. Arapaima were more likely to be located in deeper, more turbid, and higher-conductivity waters, but did not respond to temperature, pH, or dissolved oxygen concentrations. These results are consistent with previous studies of Amazon floodplain lakes

during low waters, which have identified transparency, conductance, depth, and area as important predictors of assemblage structure for fish communities (Rodríguez and Lewis, 1994, 1997; Pouilly and Rodríguez, 2004). Distance from macrophyte cover was not a useful predictor of arapaima presence, as all size classes were frequently located in both macrophytes and open water. However, small arapaima were more likely to remain closer to macrophyte edges, while medium and large arapaima ventured farther from macrophytes into open waters.

Arapaima consistently selected the deepest locations within lakes, probably because deeper areas provide increased aquatic habitat volume. Dry-season mortality rates are generally high in tropical floodplain fish populations (Welcomme, 1979; Rodríguez and Lewis, 1994), owing largely to increased predator densities, extreme water conditions, and even desiccation. Increased water volume likely promotes survival during low water periods in several ways. Particularly during droughts (e.g., due to El Niño events), deeper water offers fishes protection from extreme water quality conditions, such as increased temperature, hypoxia, and high concentrations of harmful pollutants (Schöngart and Junk, 2007). Being obligate air breathers, arapaima are not susceptible to hypoxia. However, hypoxia and other water quality extremes may indirectly affect arapaima by either decreasing abundance of prey species or leaving prey weakened and vulnerable to predation. Deeper water also corresponds with increased water volume, which would influence predation rates through decreased predator concentrations. Water transparency, which showed a significant and strongly negative relationship with arapaima presence, is known to strongly affect fish community structure in low water floodplain habitats (Rodríguez and Lewis, 1994). The success of visually-oriented predators, such as arapaima, in clearer waters can be expected to cause corresponding shifts in community structure throughout the dry season, while fish adapted to low light conditions experience higher success in more

turbid environments. Transparency also affects sunlight penetration in the water column, influencing water temperature, stratification, and energy available for primary productivity.

Castello (2008a) found that floodplain habitats containing arapaima throughout the flood cycle were significantly slower (0.12 m/s) and shallower (3.08 m) than habitats where arapaima were absent (0.15 m/s and 7.92 m). (Arantes *et al.*, 2013) found that arapaima abundance in floodplain lakes during low waters was positively related to depth, area, and connectivity; lakes possessing high arapaima abundance were deeper by an average of 1.9 m than those with low abundance. Because conductivity is influenced by many factors (e.g., temperature and nutrient concentrations), correlations observed between conductivity and floodplain fishes by this and other studies (Rodríguez and Lewis, 1994; Arantes *et al.*, 2013) deserve further research to explore the mechanisms relating conductivity to floodplain fish populations.

Inter-annual water level variability throughout the Amazon can be significant; thus dry season lake depth appears to be a key factor controlling survival of floodplain fishes. Previous studies of floodplain lakes with large arapaima populations have shown that the lowest yearly water levels records across several decades can vary up to 7 m (Ramalho *et al.*, 2009). By selecting deeper lakes to spend the dry season, arapaima increase their chances of surviving years of particularly low water levels. Given that mean lake depth in this study was only 1.5 m, while the average maximum depth was 4.15 m, it makes sense that fish would not only select deeper lakes for dry season survival, but also that they would remain closer to these deep areas to avoid becoming trapped in shallow, isolated habitats. Other fish species with life histories involving use of dry season floodplain lakes, such as tambaqui (*Colossoma macropomum*), piracatinga (*Calophysus macropterus*), and surubim (*Pseudoplatystoma fasciatum*), likely match the pattern of survival by arapaima by occupying deep areas throughout the dry season.

Although distance from nearest macrophyte cover had little effect on the presence of arapaima of all sizes, small arapaima were more closely associated with macrophytes. Several possibilities relating to ontogenetic shifts in diet and predation risk may explain the tendency of smaller arapaima to remain close to macrophyte beds. Arapaima diets change significantly across their lifespans. While juveniles and adults feed almost exclusively on other fishes, the bulk of prey items for arapaima < 1 m TL comprises insects, molluscs, and crustaceans found among the root zones of macrophytes (Queiroz, 2000). Ontogenetic shifts in diet based on gape-size limitations are a well-known aspect of many freshwater fishes (Schael *et al.*, 1991), and arapaima appear to exhibit similar patterns. Smaller arapaima likely remain close to macrophyte beds, as they support higher densities of available prey, including crustaceans, insects, and small fishes. As arapaima grow larger, they probably venture further out into open water areas to forage for larger-bodied prey. At the same time, smaller arapaima may remain closer to macrophyte beds to seek cover from a variety of predators. Previous studies have demonstrated size-specific habitat use in freshwater fishes based on the presence of predators (Holbrook and Schmitt, 1988; Persson *et al.*, 1996). When predators are present, many fish alter their foraging strategies to exploit less productive areas in exchange for reduced risk of predation. While adult arapaima possess few natural predators, individuals < 1 m TL likely follow habitat use patterns similar to other floodplain fishes. In dry season floodplain lakes, macrophytes act as nursery grounds for the majority of fish larvae (Goulding *et al.*, 1996), where the abundance of refugia and small prey items promotes their survival and growth.

### *Conservation implications*

The strong influence of community identity on arapaima presence reflects differences in the community-based management (CBM) schemes used throughout the region to conserve

arapaima populations, where differing participation and effectiveness has yielded patchy distributions of arapaima populations. Previous research has shown that successful CBM schemes in the area (i.e., systems resulting in higher arapaima density) have many of the traits related to successful self-governance (Gutiérrez *et al.*, 2011; Basurto *et al.*, 2013), such as well-defined community boundaries, rules for fisheries created and modified by local users, monitoring systems, and graduated sanctions for rule-breakers (Arantes *et al.*, 2016). Communities where these traits are absent or poorly-developed tend to have lower arapaima concentrations (Castro and McGrath, 2003; McGrath *et al.*, 2008), and thus, lower probabilities of arapaima presence. Current conservation efforts for floodplain fishes focus largely on community-level property rights, CBM schemes, and fishing agreements (McGrath *et al.*, 1993). CBM schemes would likely be improved by incorporating elements of habitat conservation, of which knowledge of the important habitats to fishes throughout their lifespan is an important component. To that end, the habitat models developed in this study reveal two key aspects for determining which floodplain habitats should be given higher conservation priority. First, fish presence is dependent upon floodplain lake habitats containing deep areas that appear to provide protection during low water events. Second, survival and recruitment of small floodplain fishes (and juveniles of larger species) is closely linked to macrophyte refugia habitats (Delariva *et al.*, 1994; Agostinho *et al.*, 2007) that are highly threatened by human activities. Deeper, macrophyte-rich lakes that persist throughout low water seasons are key habitats for floodplain fishes, including arapaima, and may be appropriate targets for conservation.

Habitat modifications to meet the needs of rapidly-expanding human populations are predicted to pose the greatest long-term threat to fish and fisheries of the Amazon (Saint-Paul *et al.*, 2000). Currently, the Amazon River contains 154 large hydroelectric dams, with another 277

dams planned for construction in the next few decades (Castello and Macedo, 2015; Zarfl *et al.*, 2015). Hydrological alterations to the natural flood pulse cycle pose a direct threat to Lower Amazon floodplain species by disrupting the timing, duration, and volume of aquatic habitat available during low water. Further, cattle ranching is the dominant land use on the Lower Amazon floodplain (McGrath *et al.*, 1993), and threatens to disrupt key floodplain habitats as forests and vegetation surrounding lakes are removed to create pastures (Zarin *et al.*, 2001). Cattle in the moving littoral zone frequently graze and trample macrophyte patches (Sheikh *et al.*, 2006), which are crucial to survival and recruitment of young arapaima and other small fishes. Reduction of macrophytes and riparian vegetation also results in increased soil erosion, which decreases water clarity through increased suspended sediment loads and reduces depth as those particulates settle out. Anecdotal information from local fishermen indicates that lakes have become steadily shallower each year as várzea development progresses. Though these claims have not been empirically tested, reduced depth is a likely result of the increased sediment loads caused by deforestation near lakes.

If sustainable fisheries are long-term management goals for floodplain lakes of the Lower Amazon, we suggest that priority be given to management practices that protect key habitats enhancing low water survival, growth, and recruitment of valued species such as arapaima. Alteration of the flood pulse by dams and disruption of vegetation controlling siltation threatens to further reduce the quality of low water habitat available to floodplain fishes. If these processes continue, there may be insufficient suitable habitat to support persistence of fish populations critical to the economy and sustenance of the Lower Amazon's human population.

Table 1.1. Habitat variable means ( $\pm$  standard error) for 13 sites in the Santarem region of the lower Amazon River. D.O. = dissolved oxygen, Cond. = conductivity, Distance = distance between an observed fish and the nearest macrophytes.

Community	Lake	Depth (m)	Relative Depth (%)	Temperature ( $^{\circ}$ C)	pH	Cond. ( $\mu$ S)	D.O. (mg/L)	Secchi (cm)	Distance (m)
Tapara-Miri	TM1	0.40 $\pm$ 0.07	0.50 $\pm$ 0.09	33.75 $\pm$ 0.34	6.54 $\pm$ 0.03	43.0 $\pm$ 0.5	6.47 $\pm$ 0.07	0.03 $\pm$ 0.00	151.8 $\pm$ 43.1
Tapara-Miri	TM2	1.21 $\pm$ 0.05	0.55 $\pm$ 0.02	31.16 $\pm$ 0.18	6.83 $\pm$ 0.07	44.0 $\pm$ 0.3	5.50 $\pm$ 0.26	0.24 $\pm$ 0.00	55.3 $\pm$ 18.1
Tapara-Miri	TM3	1.50 $\pm$ 0.01	0.84 $\pm$ 0.01	30.53 $\pm$ 0.15	6.10 $\pm$ 0.02	54.0 $\pm$ 0.9	1.54 $\pm$ 0.18	0.78 $\pm$ 0.03	8.3 $\pm$ 2.5
Tapara-Miri	TM4	1.10 $\pm$ 0.07	0.52 $\pm$ 0.03	30.71 $\pm$ 0.08	6.98 $\pm$ 0.04	52.0 $\pm$ 0.5	5.62 $\pm$ 0.23	0.16 $\pm$ 0.01	56.4 $\pm$ 14.2
Santa Maria	SM1	1.28 $\pm$ 0.02	0.71 $\pm$ 0.02	31.27 $\pm$ 0.06	6.52 $\pm$ 0.02	48.0 $\pm$ 0.8	3.08 $\pm$ 0.17	0.43 $\pm$ 0.01	15.7 $\pm$ 2.4
Centro do Aripiri	CDA1	2.43 $\pm$ 0.10	0.61 $\pm$ 0.03	31.70 $\pm$ 0.13	6.60 $\pm$ 0.02	62.0 $\pm$ 0.5	2.13 $\pm$ 0.13	1.18 $\pm$ 0.02	13.5 $\pm$ 3.0
Ilha do Carmo	IDC1	1.29 $\pm$ 0.09	0.47 $\pm$ 0.04	31.48 $\pm$ 0.18	6.54 $\pm$ 0.04	60.0 $\pm$ 1.0	2.53 $\pm$ 0.29	0.46 $\pm$ 0.04	15.4 $\pm$ 6.1
Ilha do Carmo	IDC2	0.88 $\pm$ 0.05	0.63 $\pm$ 0.04	32.43 $\pm$ 0.28	6.69 $\pm$ 0.05	75.0 $\pm$ 1.3	3.01 $\pm$ 0.36	0.29 $\pm$ 0.01	8.5 $\pm$ 4.4
Ilha do Carmo	IDC3	1.48 $\pm$ 0.05	0.59 $\pm$ 0.02	29.31 $\pm$ 0.05	6.15 $\pm$ 0.01	71.0 $\pm$ 0.8	0.50 $\pm$ 0.04	0.30 $\pm$ 0.01	3.4 $\pm$ 0.6
Ilha do Carmo	IDC4	1.04 $\pm$ 0.10	0.45 $\pm$ 0.05	32.30 $\pm$ 0.19	6.80 $\pm$ 0.03	63.0 $\pm$ 0.8	3.34 $\pm$ 0.24	0.31 $\pm$ 0.02	9.5 $\pm$ 3.6
Ilha do Carmo	IDC5	1.01 $\pm$ 0.06	0.53 $\pm$ 0.03	33.93 $\pm$ 0.09	6.94 $\pm$ 0.03	62.0 $\pm$ 1.4	3.86 $\pm$ 0.33	0.69 $\pm$ 0.02	7.7 $\pm$ 3.2
Ilha da Sao Miguel	ISM1	2.33 $\pm$ 0.37	0.44 $\pm$ 0.04	30.18 $\pm$ 0.07	7.36 $\pm$ 0.08	68.0 $\pm$ 0.5	8.39 $\pm$ 0.22	0.15 $\pm$ 0.00	33.9 $\pm$ 5.1
Agua Preta	AP1	3.59 $\pm$ 0.46	0.20 $\pm$ 0.03	30.46 $\pm$ 0.06	7.10 $\pm$ 0.02	56.0 $\pm$ 0.1	3.94 $\pm$ 0.11	0.12 $\pm$ 0.00	29.2 $\pm$ 3.8

Table 1.2. Parameter estimates ( $\pm$ standard error), P-values, cumulative model weights ( $\Sigma w_i$ ) and relative importance (rank) of habitat variables in generalized linear mixed models predicting arapaima presence in lower Amazon floodplain lakes. Ranks range from 1 (most important) to 9 (least important). Parameter estimates are given as standardized values, not in their respective measured units.

Variable	Parameter estimate	P-value	$\Sigma w_i$	Rank
Depth (m)	0.4 $\pm$ 0.16	0.0130	0.93	3
Relative Depth (%)	0.96 $\pm$ 0.24	<0.0001	1	2
Temperature ( $^{\circ}$ C)	-0.55 $\pm$ 0.34	0.1057	0.91	4
pH	-0.09 $\pm$ 0.21	0.6636	0.32	9
Conductivity ( $\mu$ S)	1.48 $\pm$ 0.75	0.0503	0.65	6
Dissolved Oxygen (mg/L)	-0.53 $\pm$ 0.32	0.0998	0.62	7
Secchi Depth (cm)	-2.21 $\pm$ 1.01	0.0281	0.85	5
Distance from Cover (m)	-0.15 $\pm$ 0.19	0.4311	0.36	8
Community			1	1
Centro do Aripiri	6.62 $\pm$ 3.73	0.0761		
Ilha do Carmo	-0.08 $\pm$ 1.14	0.9422		
Santa Maria	4.16 $\pm$ 1.11	0.0002		
Sao Miguel	-2.32 $\pm$ 0.78	0.0031		
Tapara-Miri	1.2 $\pm$ 1.15	0.2970		

Table 1.3. Habitat variable means ( $\pm$  standard error) for three size-classes of arapaima and Tukey Honest Significant Difference (HSD) pairwise comparisons across the three size classes assessed: small (S), medium (M), and large (L). HSD Columns show the p-values for pairwise tests between size classes for each variable. Bold p-values are significant.

Variable	Small	Medium	Large	HSD S-M	HSD S-L	HSD M-L
Depth (m)	1.38 $\pm$ 0.06	2.25 $\pm$ 0.21	1.73 $\pm$ 0.14	0.3955	0.8351	0.7085
Relative depth	0.66 $\pm$ 0.02	0.65 $\pm$ 0.03	0.65 $\pm$ 0.02	0.3991	0.9417	0.5610
Temperature (C)	30.78 $\pm$ 0.13	30.71 $\pm$ 0.15	30.78 $\pm$ 0.11	0.8346	0.3500	0.7104
pH	6.47 $\pm$ 0.03	6.64 $\pm$ 0.06	6.61 $\pm$ 0.06	0.5620	0.1024	0.5885
Conductivity ( $\mu$ S/cm)	58.33 $\pm$ 1.31	61.02 $\pm$ 1.09	57.80 $\pm$ 1.14	0.6407	0.5643	0.9965
Dissolved oxygen (mg/l)	2.30 $\pm$ 0.22	2.83 $\pm$ 0.31	3.18 $\pm$ 0.32	0.2548	0.3243	0.9734
Secchi Depth (cm)	0.39 $\pm$ 0.02	0.49 $\pm$ 0.04	0.45 $\pm$ 0.03	0.5060	0.2802	0.9301
Open water distance	12.96 $\pm$ 2.09	29.07 $\pm$ 3.13	30.33 $\pm$ 2.94	<b>0.0332</b>	<b>0.0058</b>	0.8597

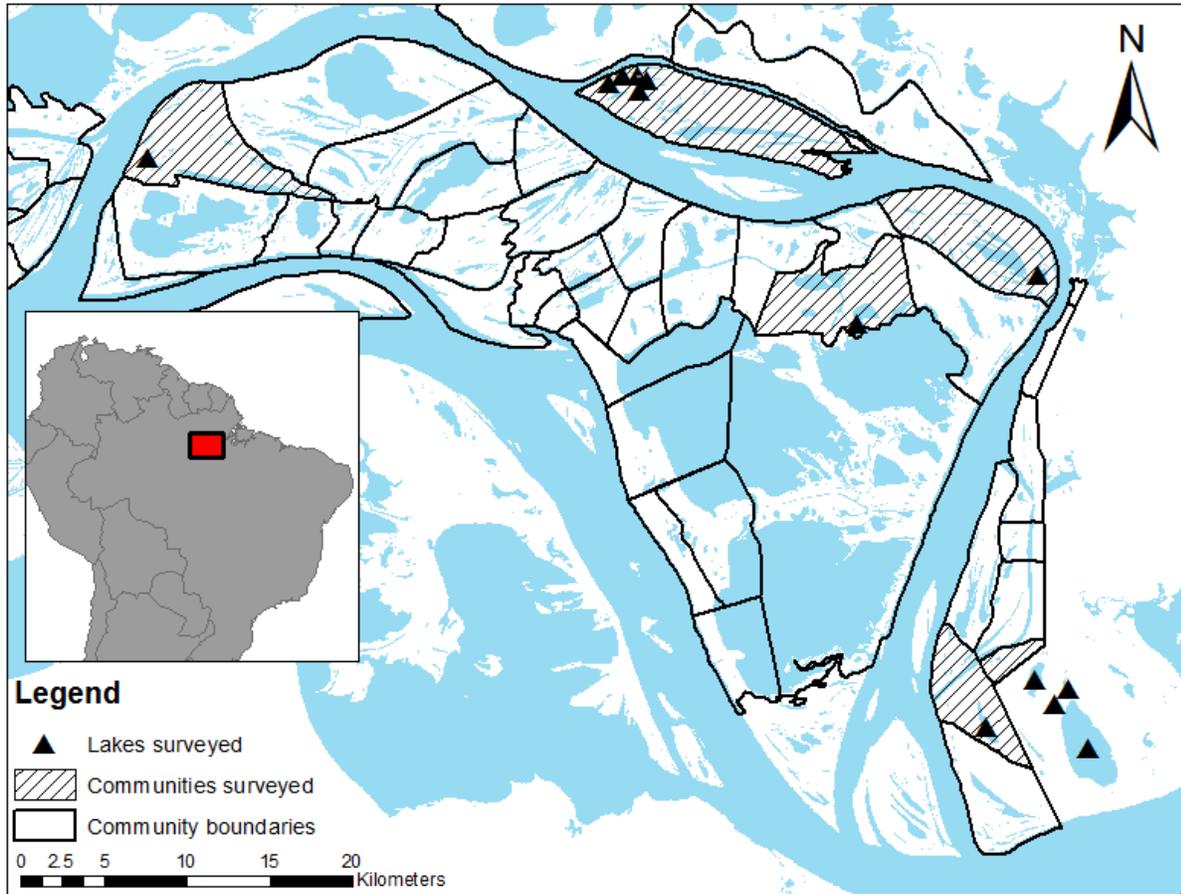


Figure 1.1. Map of the lower Amazon region depicting fishing community boundaries and sampling locations.

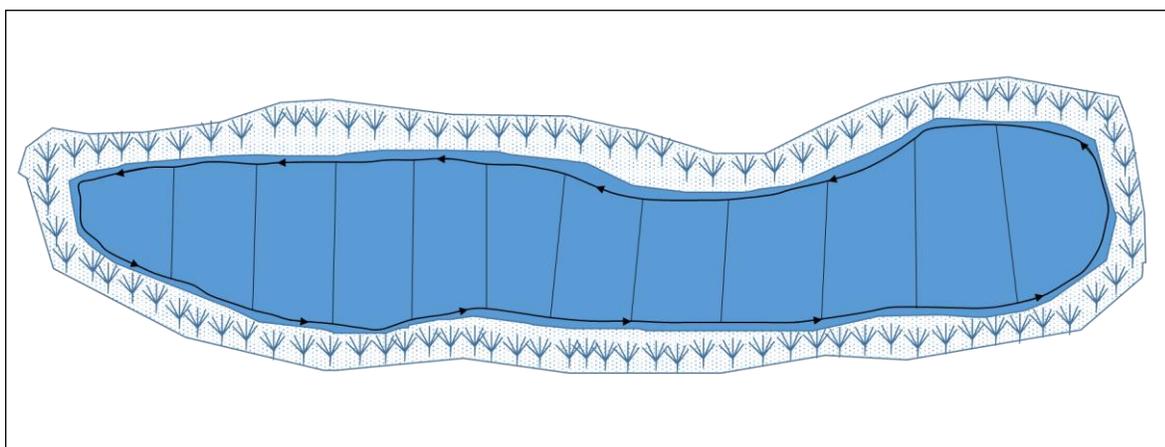


Figure 1.2. Schematic representation of a typical várzea lake in the lower Amazon. Solid colored area indicates open water, stippled area indicates floating aquatic macrophytes. Surrounding areas included patches of aninga, dry forests, and cattle pastures (not pictured). Black lines and arrows indicate the direction and path traveled during data collection.

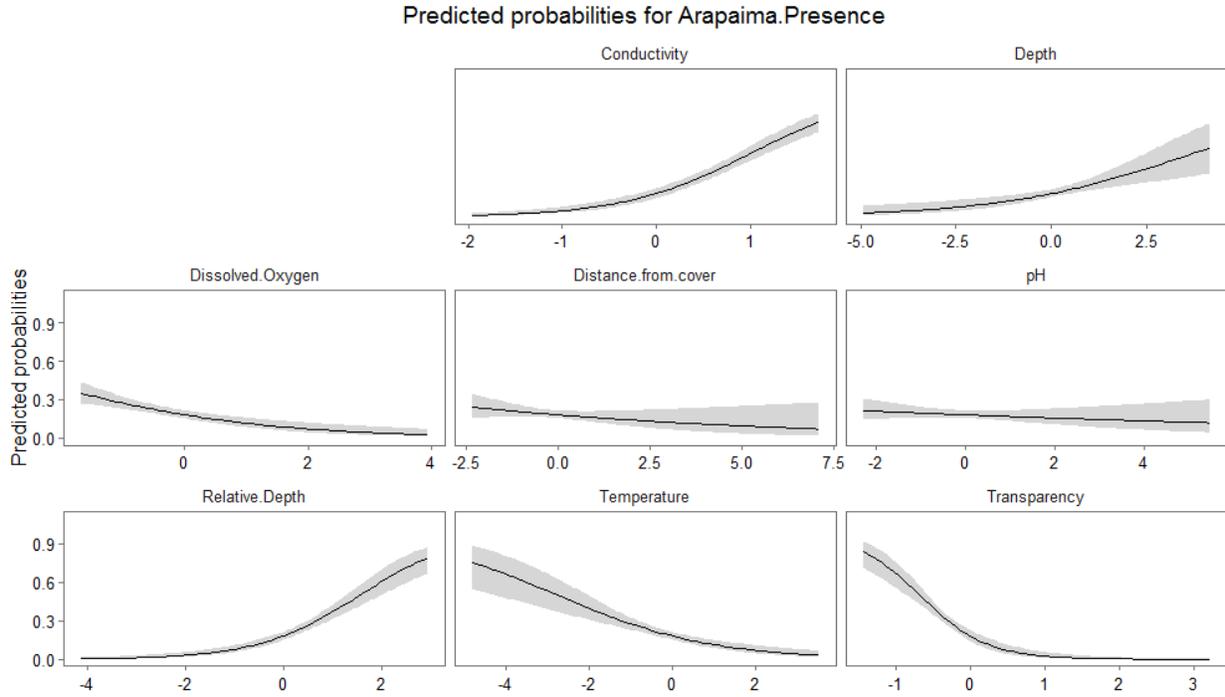


Figure 1.3. Plots showing the predicted probabilities of arapaima presence based on each of the eight habitat predictors measured. All plots are scaled based on the standardized estimates for the spatialized variables. 95% Confidence intervals are shown in gray.

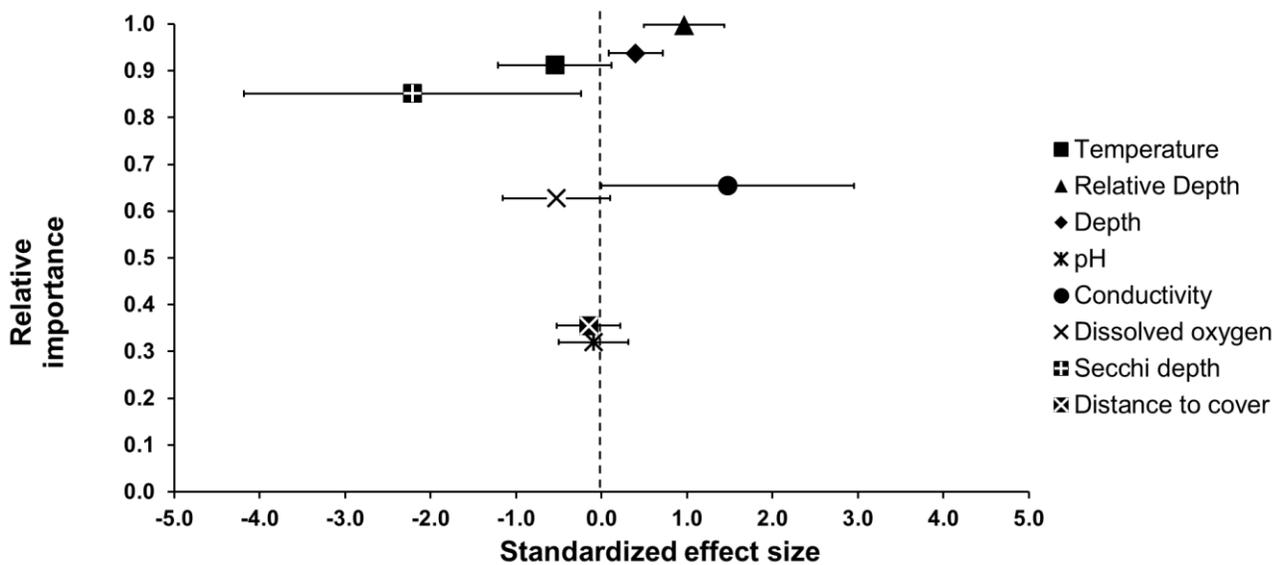


Figure 1.4. Plot showing standardized effect size and relative importance to arapaima occurrence for each of the eight habitat variables measured. Error bars for each point show 95% confidence intervals for estimates.

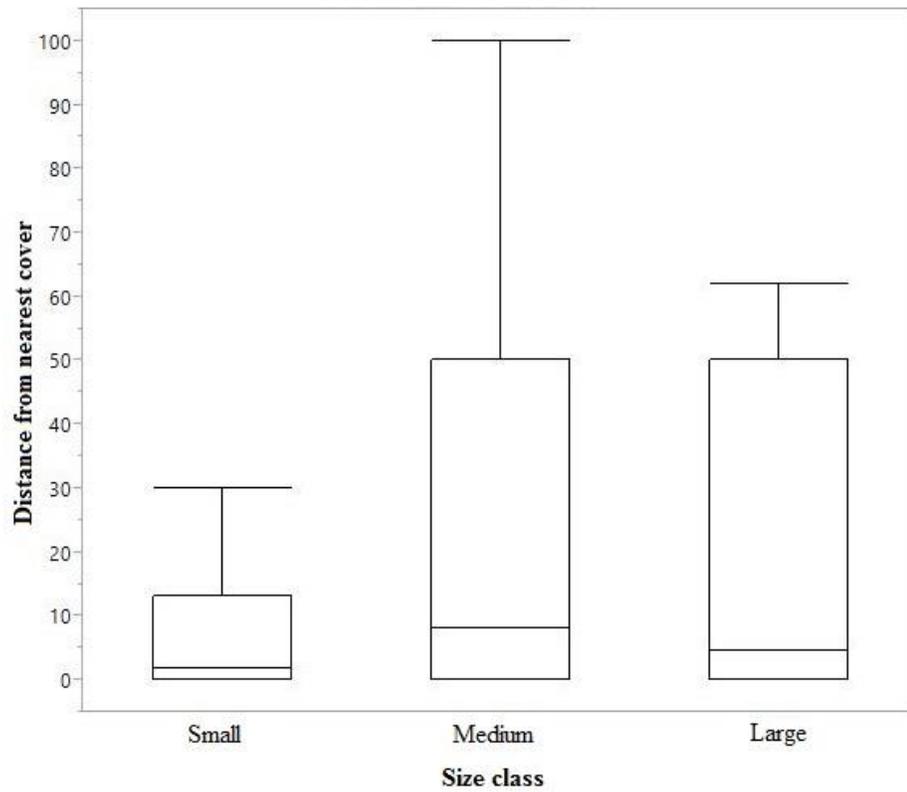


Figure 1.5. Quantile plot of distance from nearest cover for small, medium, and large arapaima. Small arapaima were significantly different from medium and large arapaima, while medium and large arapaima were not significantly different from each other.

**Chapter 2.** A landscape approach to modeling resource abundance in social ecological systems:  
a case study of arapaima fisheries in the Lower Amazon River

**Abstract**

Understanding patterns of sustainable use for natural resources governed by community-based management (CBM) schemes is a topic of increasing research interest. Social ecological systems (SES) frameworks have been a popular method for interdisciplinary research linking human and environmental influences to resource systems. However, few studies have quantitatively linked human and ecological variables in a spatially-explicit manner to assess patterns of resource abundance and management outcomes. The goal of this study was to examine the effects of three factors (human governance, landscape habitat, and spatial structure) on abundances of arapaima *Arapaima spp.* and determine the extent to which each effect controls abundance when considered simultaneously. Three independent linear models were developed relating governance, landscape habitat, and spatial structure to arapaima abundances in dry season lakes, and variation partitioning was used to examine the unique and joint influences of the three models. All three models explained large proportions of the variability observed in arapaima abundances. Governance and habitat contributed equally in explaining variability, and overlapped significantly when considered simultaneously. Spatial structuring was a significant influence on governance, habitat, and variability in arapaima abundances. This study reveals that patterns of resource abundance are strongly influenced by human, environmental and spatial effects, and researchers should be wary of assessments excluding any individual component. Failing to simultaneously model all three components may lead to overestimations of the importance of individual factors in controlling resource abundance.

## **Introduction**

Sustainable use of natural resources necessitates an interdisciplinary approach to describe human and environmental interactions because single disciplines cannot provide a complete understanding of the complex nature of environmental problems. In order to describe complex environmental problems, researchers have increasingly relied on frameworks like the social-ecological systems (SES) model (Ostrom, 2009), which guides assessments of the multidimensional components contributing to sustainable resource use and management. Recent studies have shown that many SES studies focus mainly on social aspects and fail to sufficiently incorporate important ecological variables into assessments of resource systems (Epstein *et al.*, 2013; Leslie *et al.*, 2015; Vogt *et al.*, 2015). Similarly, ecological research has commonly ignored integrations of human influences and environmental drivers. The prevailing lack of effective integration of social and ecological sciences is illustrated by a recent meta-analysis of SES research, which found that quantitative methodologies combining social and ecological variables were present in less than 10% of 120 studies reviewed (Rissman and Gillon, 2016). There is a need for analytical mechanisms linking SES frameworks to traditional methods of ecological inquiry to accurately describe the underlying drivers that support sustainable ecosystems.

A central tenet of SES is the need to match scales of ecological processes to those of human institutions in order to facilitate governance (Wilson, 2006). Human and natural systems are both spatially organized in relation to a multitude of complex interacting factors. For example, fisher communities are often distributed along rivers, lakes, and oceanic coasts following the spatial distribution of fishing grounds and fish populations. Managing these fisheries requires allocating tasks like rule creation and enforcement at spatial scales that match

the geographic distribution of the harvested fish populations. Similarly, creating suitable management rules may not be sufficient if the scale of management itself is incorrect. Here, we test the use of proper spatial scale as a mechanism to link human and environmental drivers of resource abundance in ways that enhance sustainable fishery management. We examine the case of arapaima fisheries of the lower Amazon River, in the state of Pará, Brazil, because it is a well-documented example of how community-based management (CBM) strategies can be applied to fisheries throughout a landscape of spatially-explicit fishing communities (McGrath *et al.*, 1993, 2008).

Understanding the role of spatial structuring in patterns of ecological datasets has been an increasingly fundamental component of ecological research in recent decades (Legendre and Fortin, 1989; Peterson and Parker, 1998; Borcard *et al.*, 2004). Numerous methods are now available to incorporate the geographic coordinates of observations directly in statistical models relating ecological variables to species assemblages (see Legendre and Troussellier, 1988; Legendre and Fortin, 1989; Leduc *et al.*, 1992 for but a few of many examples). In cases where environmental variables and species assemblages share a common spatial structure, the amount of variation in species data they explain may be redundant, and therefore lead to overestimation of the true proportion of variation explained when both components are included (Legendre and Troussellier, 1988). Borcard *et al.* (1992) developed an approach (hereafter referred to as variation partitioning), allowing researchers to partition the proportion of variation in a response variable into components uniquely explained by each independent variable dataset, components jointly explained by the datasets, and a component explained by none of the datasets (i.e., unexplained variation). Variation partitioning is now widely-used in ecological research, most commonly to separate the influence of environmental and spatial variables on multivariate

species datasets. In these analyses, the proportion of variation explained uniquely by spatial variables, as well as the proportion of unexplained variation (which is often high), can potentially be explained by other variables not considered in the model (Borcard *et al.*, 1992). Though it seems likely that human influences on species assemblages may be important contributors to the unexplained variation or the uniquely spatially-explained variation, ecological studies frequently do not incorporate human variables into modelling of species patterns (Rosa and Dietz, 1998; Liu *et al.*, 2007).

Research linking human effects to environmental systems often utilizes a different approach to considering the spatial effects, in which spatial scaling is primarily defined in terms of hierarchical human institutions managing natural resources (Cumming *et al.*, 2006) (Figure 2.1). In ideal systems, the human institutions governing natural resources are matched to the resources at the most effective scale (Folke *et al.*, 2005). For example, a federal government would likely be an inappropriately large institution for developing specific rules regarding an individual lake fishery, while a thousand individual community groups throughout a country would be too unwieldy to conduct international agreements governing trade with other countries. In this sense, nested tiers related to spatial scale of human organizations and natural resource systems are an integral part of social science research, but they do not incorporate the quantitative spatial effects of resource systems into models as explicitly as variation partitioning in ecological studies. Interdisciplinary research linking human and environmental effects in SES is largely skewed in favor of social science approaches (Epstein *et al.*, 2013; Vogt *et al.*, 2015), which has resulted in many of the resulting models considering spatial effects in a less quantitative manner than may be warranted.

This study uses arapaima (*Arapaima spp.*) fisheries to examine the usefulness of spatial structuring variables to elucidate the interactive effects of community-based management and landscape-scale habitat factors on the distribution and abundance of this highly-exploited fish taxa. Arapaima are historically the most important fish to Amazon fisheries. They are most commonly found in floodplain lake systems, where they migrate seasonally among several floodplain habitats, including shrub, forest, and macrophytes, in response to water level variations. In Brazil, management of arapaima in these environments has historically devolved into a typical ‘tragedy of the commons’ (Hardin, 1968) situation enabled by an open-access regime in which all citizens have equal rights to use aquatic resources. The Brazilian government has attempted to reverse declining arapaima population trends by establishing minimum size limits (1.5 m total length (TL)), closed seasons (December–May), and even moratoria in some states. These top-down regulations have proven largely ineffective as the federal and state institutions implementing them lack sufficient local-scale monitoring and enforcement resources (McGrath *et al.*, 1993). As a result, as much as 77% of arapaima catches are illegal (Cavole *et al.* 2015), and in many areas arapaima populations are widely overexploited and even depleted to the point of localized extinctions due to their high economic value (Castello *et al.*, 2015a).

Successful arapaima management now depends largely on cooperative, bottom-up, CBM schemes in which higher levels of government (i.e., state and federal agencies) place control of fishery resources in the hands of local users (McGrath *et al.*, 2008; Castello *et al.*, 2009). The difference in the spatial scale of these management approaches is striking. For example, management rules like the moratorium on arapaima fishing in the State of Amazonas applied across the entire 1.5 million km<sup>2</sup> area of the state, but were enforced by only a handful of government employees. By contrast, local scale CBM schemes operate at a community level

(generally  $\sim 25 \text{ km}^2$ ), and are enforced by the community members. In these CBM systems, local fishers self-impose closed seasons, gear restrictions, and size limits of catch in order to increase the abundance of local fish populations and to address concerns over food and income security. When implemented successfully, arapaima CBM caused up to 23-fold increases in population sizes within a decade of implementation, in part due to the biological traits of arapaima which confer to them high rates of population growth (Castello *et al.*, 2011). These CBM systems provide a unique opportunity for understanding the relationships between management and environmental factors resulting in sustainable fisheries use. The combination of the arapaima's high economic value and their fast population responses to conservation measures makes CBM an ideal system for studying the relationships between people, resources, and landscapes in SES.

In order to test the use of spatial structuring as a mechanism to link and compare the relative magnitudes of human and environmental factors affecting arapaima population size, we (1) develop independent quantitative models of arapaima population size as a function of landscape, governance, and spatial factors, and (2) utilize variation partitioning to assess the variation in fish abundances that can be explained uniquely and jointly by each of the three components. We expect that the combined model incorporating human, environmental, and spatial influences will provide significantly improved explanatory power as compared to models of individual components. Strongly shared variation between all three components would suggest that space plays an important role in structuring landscape and governance factors. Determining the magnitude of influence from each component is an important step in facilitating continued sustainability of successful CBM systems and in developing measures to promote sustainability in areas where populations are currently depleted.

### *Study Area*

The study was conducted in floodplain habitats along approximately 180 river km of the lower Amazon River in Pará State, Brazil (Figure 2.2). The lower Amazon ecosystem comprises the nutrient-rich waters of the main river channel flanked by seasonally-flooded habitats, including forested levees, grasslands, and a series of lake networks in the floodplain interior. Though the floodplain was once heavily forested, habitat alteration is now prevalent; 56 % of the floodplain was deforested between 1970 and 2008 (Renó *et al.*, 2011). The yearly change of river height from dry season to flood season is ~ 7 m (Sioli, 1984). In the dry season, aquatic habitats are limited to the main river channel and permanent floodplain lakes (Figure 2.3) at their lowest water levels (hereafter, “dry season lakes”). During the rising water period (approximately December through May), the waters within main river channels progressively rise, flooding the surrounding habitats and continuously expanding across the landscape until the peak flood stage, at which point the lower Amazon comprises a single aquatic landscape. The seasonally-flooded zones flood based on topography, beginning with low-lying grasslands habitats containing numerous perennial semi-aquatic macrophyte species (Table 2.1). Shrub and forested habitats are the next areas to flood, followed finally by mid- to high-elevation grasslands – many of which are denuded areas formerly containing forests. Each habitat type provides forage, refugia, and reproductive habitats for many floodplain fishes (Goulding, 1980; Goulding *et al.*, 1996). Following peak flood stage, during which fishes occupy these highly productive seasonal habitats, the process reverses. As water levels decline from August to December, floodplain habitats shrink until once again the only aquatic habitats remaining are the main river channels and dry season lakes.

Fisheries in the lower Amazon constitute a significant proportion of the local economy and also play a vital role as a protein source for much of the human population. The majority of

commercially-important Amazon fishes utilize river-floodplain habitats throughout the year (Castello *et al.*, 2013), where they take advantage of the seasonality in resource availability driven by the flood pulse (Lowe-McConnell, 1987; Castello, 2008a). During the flood season, floodplain fishes occupy the highly productive flooded forest habitats adjacent to lakes (Goulding, 1980), where predation risk is low owing to the diffuse concentrations of prey species throughout refugia (Saint-Paul *et al.*, 2000). As waters recede into the dry season, fish are forced to migrate out of the floodplains into either permanent lakes or main river channels. Decreased habitat availability during the dry season results in a concentration effect for many populations, leaving them susceptible to overfishing. Fishing pressure is maximized during the dry season to exploit these concentrated populations, making governance an important driver of long-term fishery sustainability.

Managing the floodplain fisheries of the lower Amazon has traditionally been problematic due to the open-access nature of fishing grounds established by Brazilian law. Local-scale attempts by individual communities to conserve or manage fishing grounds were thwarted by city-based and commercial fishers, who quickly depleted thriving stocks (Smith, 1985; Almeida *et al.*, 2001). In response to the growing issue of floodplain resource use, CBM schemes multiplied in the region, taking two main forms: fishing agreements, which occur in ~40% of local communities, and Agro-extractivist Settlement Projects (known as ‘PAEs’), which occur in ~60% of communities. Fishing agreements were established in the 1990s through collaborations between local communities, government agencies, and non-governmental organizations. Fishing agreements consist primarily of rules – recognized by higher levels of government – restricting fishing gear, locations, and seasons within local fisheries. These restrictions make fishing in such areas unappealing to non-local, city-based fishers, effectively

restricting access to only those local fishers willing to harvest under the established regulations. PAE communities have collective land concessions, which were formally established in 2011 in cooperation with the Brazilian agrarian reform agency as a means for sustainably managing natural resources within their respective areas (McGrath *et al.*, 2008). Both PAE and fishing-agreement communities utilize representatives who implement fishing rules and bring unresolved issues from the community level to the Regional Fisheries or PAE Councils, which represent the next higher level of governance. The communities studied here range in size from 40 to 130 families, most of which rely on fishing for subsistence and income (McGrath *et al.*, 2008).

Arapaima are a primary focus of CBM schemes in the region because they have high social, cultural, and economic value, and they possess several life history traits conducive to bottom-up conservation schemes. Arapaima have historically been overfished, as they possess high market prices, grow to three meters in length and 200 kg in weight (Castello and Stewart, 2010; Castello *et al.*, 2015b), and are easy targets for fishermen because they must surface every 15 minutes to breathe air. Recent arapaima population recoveries achieved by CBM schemes have shown great promise (Castello *et al.*, 2009, 2011; Arantes *et al.*, 2010). CBM schemes for arapaima have thus become increasingly popular in the region.

## **Methods**

For the lower Amazon region near Santarem, we developed a comprehensive dataset including arapaima population data for 73 floodplain lakes, satellite-derived data on habitat classifications and macrophyte presence, and eight indicators of governance measured for 83 floodplain fishing communities. To model arapaima population sizes in floodplain lakes as a function of landscape, governance, and spatial factors, we first identified sets of candidate

explanatory variables based on previous research. We developed quantitative indicators of each variable identified that could be measured for each of 73 floodplain-lake arapaima populations throughout the study area. We used model selection procedures to identify the most important landscape and governance variables. In order to assess the role of spatial structuring as a linking mechanism for the governance and landscape factors, first we developed an independent spatial model of arapaima abundance using principal coordinates of neighbor matrices (PCNM) analysis. Then, we integrated the spatial, landscape, and governance models using variation partitioning analysis to quantify the unique and joint contributions made by the three models in terms of explaining variability in arapaima abundance across all lakes.

#### *Arapaima abundance data*

We estimated arapaima population sizes in 73 floodplain lakes using data collected from arapaima management censuses conducted from 2004 – 2014 (Figure 2.5). Arapaima are unique among highly-exploited floodplain fishes in that their obligate air breathing facilitates a relatively simple, inexpensive method for determining population sizes. Trained fishers observe lakes for a set time and visually count the number of adult and juvenile arapaima surfacing to breathe using the standardized method of Castello (2004). Population estimates using this methodology have been found to vary within ~ 10% of true values (see details in Castello 2004). We assembled arapaima population data records from the Instituto de Pesquisa Ambiental da Amazonia (IPAM), who has collected these data together with communities, NGOs, and researchers during the dry season, when arapaima populations are confined to the isolated dry season floodplain lakes prevalent throughout the region (Castello *et al.*, 2015b). We accounted for inter-annual variability in abundances by using the average census count over multiple years,

when available. We  $\log_{10}$ -transformed the abundance data prior to all modeling procedures in order to achieve an approximately normal distribution and meet the assumptions of linear models.

### *Landscape Habitat Model*

We utilized a modelling approach delineating flood-season habitat availability for each dry season lake by applying aspects of circuit theory (McRae *et al.*, 2008) to create a resistance surface for the landscape. In traditional applications of circuit theory to landscape connectivity, the potential movement of organisms is modelled analogously to electricity moving through paths of least resistance. Thus, habitats hypothesized to inhibit movement are assigned higher resistances (Spear *et al.*, 2010), while corridors and other areas facilitating movement are assigned lower resistances. Using these resistance values for each habitat type, paths of least resistance between populations are purported to represent the most likely connections between populations or habitats (Figure 2.4).

Habitat availability for arapaima includes only habitats that are sufficiently inundated. Rather than assign resistance values based on hypothetical utility for migrating fishes to habitat classes of the lower Amazon, we created a resistance surface based on the timing and duration of flooding for each habitat type. Because topography is associated with habitat types, we determined the order in which habitats became inundated throughout the flood cycle. We assigned a cost distance to each of the seven functional floodplain habitat types present (Table 2.1), with areas that are infrequently inundated mapped as more resistive (i.e., lower probability of movement or use) than areas that are flooded for extended periods and connected to

surrounding aquatic habitats. Using this information, we delineated an “accessible” landscape around each dry-season lake based on the accumulated cost distance along all possible paths until a specified cutoff value was reached. The cutoff value reflected arapaima movement ranges described by Crossa (2003).

For each landscape delineated around a dry-season lake, we used Geographic Information System (GIS) software (ArcMap 10.2.2) and Fragstats (version 4.2.598) (McGarigal *et al.*, 2012) to calculate landscape metrics describing the composition and arrangement of floodplain habitats. We calculated three parameters (Table 2.2) for each habitat type (Table 2.1) to quantitatively describe the composition and arrangement of floodplain habitats. These parameters were selected based on previous knowledge of arapaima habitat associations (Castello, 2008a; Arantes *et al.*, 2013; Richard, 2016): Class Area (CA), Clumpiness (CLUMPY), and the area-weighted mean Euclidean Nearest Neighbor distance (ENNAM) between patches of the same type.

Macrophyte patch distribution was based on a 30-m resolution dataset of presence/absence collected during the rising water phase of the flood pulse (when macrophyte presence is maximized) over a five year period coinciding with the collection of the arapaima density data (2007 – 2011). We classified locations into three groups for analysis: areas where macrophytes were never present, areas where macrophytes were present irregularly (one to three out of five years observed), and areas where macrophyte stands consistently developed (four or five out of five years observed). The two parameters calculated for macrophyte coverage were Percentage of Landscape (PLAND) and Clumpiness (CLUMPY).

Following calculation of the 27 potential variables ([7 habitat types x 3 parameters] + [3 macrophyte classifications x 2 parameters]), variables were selectively omitted if they were

deemed nonsensical (e.g., main channel areas always comprised a single patch, making ENN-AM meaningless for channel habitats). We then screened the remaining candidate variables and removed variables for multicollinearity based on a maximum allowable  $r > |0.7|$ . Six variables were removed from consideration, and subsequent model selection procedures were conducted using 21 candidate landscape habitat variables. A subset of the best landscape habitat predictors of arapaima abundance was developed using an information theoretic (IT) approach based on the stepwise-forward variable selection in the *stepAIC* function from the *MASS* package (Venables *et al.*, 2002) of R (Version 3.2.3) (R Core Team, 2014). We started with a null model containing no landscape variables and added the variable that resulted in the greatest reduction in Akaike's Information Criterion (AIC). Variables were iteratively added until no further reduction could be obtained, at which point the model represented the best explanation of variation in arapaima abundances that could be obtained from the considered landscape variables.

### *Governance Model*

In order to model arapaima abundances as a response to governance factors, we used data from Arantes *et al.* (2016) on a set of eight governance factors hypothesized to influence the abundance of arapaima in floodplain lakes. Governance factors reflected the eight institutional design principles proposed by Ostrom (1990). Research on these principles over recent decades has led to the widely accepted conclusion that they are well-supported by empirical evidence (Cox *et al.*, 2010). The foundation of Ostrom's principles includes the presence of a series of factors, including well-established resource system boundaries, autonomy of users to create and adapt governance rules at a local scale, capability of monitoring the resource and behavior of users, punishments for rule offenders that increase with the frequency and severity of

transgressions, and affordable means of conflict resolution for disputes. Adherence to these principles was measured for all communities in which we had arapaima abundance data (each principle is summarized in Table 2.3). Data for each principle were measured using indicators that were developed specifically for understanding the influence of Ostrom's design principles on the abundance of arapaima in dry season lakes. We screened and removed variables for multicollinearity based on a maximum allowable  $r > |0.7|$  and each of the remaining variables was assessed for normality. Two of the eight variables in the CBM data matrix (I7 and I8) were excluded from the analysis because they were singular (i.e., all values were the same) for the communities assessed by this study. Each variable was then considered as a potential candidate for inclusion in models relating measures of governance to arapaima abundances. We followed the same IT approach described for the landscape habitat models, using stepwise-forward variable selection, to determine a best subset of governance variables.

### *Spatial Model*

To assess the extent to which arapaima population sizes in dry season floodplain lakes were spatially correlated, we conducted a Principal Coordinates of Neighbor Matrices (PCNM) analysis using the *PCNM* function from the *PCNM* package (Legendre *et al.*, 2013) of R. PCNM analysis models the spatial arrangement of the data points (dry-season lakes) within the landscape based on their geographic coordinates by creating quantitative descriptors (PCNM axes) that can be statistically modeled alongside other variables. The analysis utilized in this study was conducted following standard procedures for PCNM, in which the threshold distance for defining sites as neighbors was truncated to the minimum distance needed to keep all sites connected. Pairwise distances between sites greater than this cutoff value were calculated as four times the cutoff value. Variable selection procedures were not utilized for determining a best

subset of spatial variables because the PCNM axes collectively represent the spatial structuring in the dataset at different scales. Instead, all positive and significant eigenvectors ( $p < 0.05$ ) calculated from the pairwise matrix of site locations were retained as variables representing the spatial component of the dataset.

### *Variation Partitioning*

To assess the variation in arapaima abundances that can be explained uniquely and jointly by each of the three components, we conducted variation partitioning using the *varpart* function from the *vegan* package (Oksanen *et al.*, 2015) of R. We then used partial linear regression to estimate the proportions of variation in arapaima abundance (measured as adjusted- $R^2$ ) uniquely attributable to each set of explanatory variables after the other sets of variables were taken into account (Legendre and Legendre, 2012). The total inter-lake variation in arapaima abundances was partitioned into eight independent components: (i) three ‘pure’ components explained uniquely by landscape habitat, governance, or spatial variables, (ii) three two-way ‘shared’ components consisting of the proportion of variation shared by each pair of the three data matrices independent of the third, (iii) one three-way interaction of the variation ‘shared’ among all three data matrices, and (iv) unexplained variation, which is the fraction explained by none of the three matrices. Large proportions of variation explained by the pure components would indicate that they possess high individual relative importance, while large proportions shared with space would indicate the importance of spatial structuring in determining the influence of governance or habitat variables. Because the union of three independent models’ results involves a large number of variables included in the overall model, all correlations were reported using adjusted- $R^2$  to penalize over-fitted models.

After computing the proportion of variance uniquely attributable to each of the three data matrices, we calculated standardized partial regression coefficients and partial  $r^2$  (Neter *et al.*, 1996) to compare the relative importance of individual variables within each matrix. We determined these values by regressing the variables from each data matrix on the residuals obtained from a regression of the other two matrices on the abundance of arapaima. This residual analysis enabled us to examine the individual components of each model contributing uniquely to the overall explanation of variance.

## **Results**

### *Landscape, Governance, and Spatial Models*

Model selection procedures relating landscape habitat variables to arapaima abundances yielded a five-variable model consisting of shrub habitat aggregation, inter-patch distance for forest habitats, total dry-season lake area, and aggregation of both regularly- and irregularly-present macrophyte patches (Table 2.4). Of these, only aggregation of irregularly-present stands of macrophytes was non-significant ( $p = 0.10$ ). Aggregation of shrub and regularly-present macrophyte patches were both positively correlated with arapaima abundances (i.e., concentrations of these habitat types into large, uniform patches was associated with higher arapaima abundance), while forest inter-patch distance and total lake area were negatively correlated with abundances (i.e., landscapes with larger volumes of open lake habitat and longer distances between patches of forest contained fewer arapaima). The five-variable landscape habitat model explained 51.3% of the variation in arapaima abundances among lakes.

The governance model comprised three of the six variables considered: collective action arrangements (I3), monitoring system (I4), and graduated sanctioning (I5). I4 was highly

correlated with both defined boundaries (I1) ( $r^2 = 0.72$ ) and congruence between rules and local conditions (I2) ( $r^2 = 0.90$ ), thus only I4 was included during model selection procedures. I3 and graduated sanctioning (I5) were best modeled as ordinal variables containing three levels, therefore the final governance model contained five variables describing three governance factors. All factors included in the governance model were positively and significantly correlated with arapaima abundances (Table 2.4), and they collectively explained 51.8% of variation in arapaima abundances.

PCNM analysis of the spatial components yielded 42 total eigenvectors (PCNM axes). Of these, the spatial factors model comprised only the ten PCNM axes that were both positive and statistically significant. Five of the ten axes included in the model were significantly correlated with arapaima abundances (Table 2.4).

### *Variation Partitioning*

The full model combining all variables selected for the three individual models included 20 variables (10 spatial PCNM axes, five landscape habitat variables, five governance variables) and explained 71.0% of variation in arapaima abundances (Figure 2.6). Individual landscape and governance models were relatively balanced, containing five variables each and providing similar explanatory power. The landscape habitat model contributed a unique 13.0% explanatory power when governance and spatial factors were considered, and shared 7.8% with spatial factors independent of the governance variables. Governance variables uniquely contributed 12.0% explanatory power when spatial and landscape factors were considered and shared 9.2% with spatial factors independent of the landscape factors. The spatial factors model alone

explained 44.3% of variation in arapaima abundances, but contributed no unique explanatory power. The single largest component of explanatory power was the three-way shared intersection between the landscape, governance, and spatial models, with 28.7% variation explained. The shared variation between landscape habitat and governance variables was just 2% when considered independently of space, but was 29% when also shared with spatial variables.

## **Discussion**

The analysis yielded two key findings explaining the variation in arapaima abundances throughout the study area. First, as evidenced by the large (29%) three-way component of shared variability, spatial structuring played an important role in the individual components controlling arapaima abundance. Second, arapaima abundances were explained equally by landscape habitat and governance variables, both when modeled alone (51.3% and 51.8%, respectively) and together (13.0% and 12.0%, respectively). Considering either the governance or landscape habitat variables independently would lead to overestimations of variable importance, as modeling them together revealed that a large proportion of the variation explained (31%) was shared between the two. Further, when spatial variables representing spatial structuring were included as a third component to the human-environmental model, the overwhelming majority of the shared explanatory power (29% of the total 31% shared) was explained as a common spatial structuring shared between the variables. Accounting for spatial structuring also changed the relative importance of individual variables within each of the component models. For example, while graduated sanctioning (I5) and average inter-patch distance for forests (ENNAM-Forest) had the smallest and second smallest coefficients in their respective individual models, they were the largest contributors to the *unique* variability explained by their components in the combined

partitioning analysis (i.e., after space was accounted for, they become the most important variables). Failing to calculate a unified model simultaneously assessing governance, landscape habitat, and spatial effects would therefore not only have led to overestimation of the importance of each component, but would also result in incorrect identification of the most important individual landscape or governance variables. It would seem, therefore, that spatial analysis does serve as a mechanism to frame simultaneous analysis of human and environmental variables.

The landscape habitat features found to influence arapaima abundances provided further evidence of the importance of spatial structuring. Four of the five variables selected were related to the arrangement of habitats within the landscape, rather than volumes or percentages of habitat types. Landscapes can be characterized in terms of the area, volume, and the spatial arrangement of those patches (Turner, 1989; Dunning *et al.*, 1992), thus factors such as total habitat area may be less important in sustaining populations than the arrangement or connectivity of key habitat types (Taylor *et al.*, 1993). The strongest landscape habitat predictors of arapaima abundances were average inter-patch distance for forests habitats (ENNAM-Forest, standardized regression coefficient =  $-0.87$ ,  $p < 0.0001$ ) and aggregation of shrub habitats (CLUMPY-Shrub, standardized regression coefficient =  $0.88$ ,  $p < 0.0001$ ). Flooded forests and shrubs are known to be important habitats for arapaima (Castello, 2008a, 2008b). Arapaima build nests near lake margins under forested levees during the rising water period. Following spawning, male arapaima guide the newly-hatched young throughout the flooded forest areas for several months, where they grow and feed on the rich nutrients provided from fruits, insects, and fish of the forests (Queiroz, 2000; Castello, 2008a, 2008b). Shorter distances between forest patches would provide arapaima enhanced opportunities to forage throughout a variety of forest areas, particularly when attempting to minimize exposure of newly-hatched young to higher currents

and avian predators associated with open water areas. Similarly, large aggregated patches of flooded shrub habitats likely supply fruitful foraging areas for arapaima, while also providing refugia from predators for smaller individuals.

Floating macrophytes had a positive effect on the abundance of arapaima. They are known to be important habitats for arapaima, particularly during earlier life stages when they are utilized more frequently (Richard, 2016). The bulk of prey items for arapaima < 1 m TL comprises insects, molluscs, and crustaceans found among the root zones of macrophytes (Queiroz, 2000). The aggregation of regularly- and irregularly-present macrophyte areas (CLUMPY-RegMacro, CLUMPY-IrrMacro) was positively related to arapaima abundances, though only CLUMPY-RegMacro was statistically significant ( $p$  0.0106). The only habitat variable best modeled in terms of volume alone was total lake area (CA-Lake), which was negatively correlated with arapaima abundances. Previous studies have shown that larger arapaima populations are found in larger, deeper lakes (Arantes *et al.*, 2013; Richard, 2016), but it is important to note that CA-Lake is a measure of total open water lake area within the landscape, not the size of an individual lake containing arapaima. The negative correlation with total lake area found here is likely related to the fact that larger lakes in the area are more frequently visited by commercial fishermen, making them contentious areas where conflict over CBM rules has resulted in depleted catches for all species (Isaac and Ruffino, 2007). It is also possible that in areas where dry-season lakes are abundant, the total concentration of arapaima may be diffuse when compared to a landscape containing only 1-2 suitable lakes, which could result in the observed negative relationship between arapaima abundance and CA-Lake. All other significant relationships between arapaima abundances and landscape habitat indicated that larger, more aggregated habitat patches of macrophytes, shrubs, and forests supported larger

populations. Our findings align with previous studies, which have shown that vegetated floodplain habitats such as flooded forests, shrubs, and macrophytes are important for floodplain fish growth, survival, and reproduction (Fernandes, 1997; Castello, 2008a; Arantes *et al.*, 2013). The flooded vegetation of the Amazon provides some of the most biologically-productive habitats in the world (Goulding *et al.*, 1996), therefore it makes sense that arapaima and other fishes would likely thrive in landscapes providing large aggregations of shrubs, forests, and macrophytes. These habitats control numerous factors influencing floodplain fish distribution, including dissolved oxygen concentrations, food resource availability, and predation success (Agostinho *et al.*, 2007).

We identified collective action arrangements (I3), monitoring system (I4), and graduated sanctioning (I5) as key components of community governance directly associated with arapaima population sizes. These three components of governance established that arapaima populations were monitored, rules regarding arapaima fishing were created with participation from all community members, the rules were enforced by the community members themselves, and punishments were enforced for rule-breaking individuals. The strong collective presence of these mechanisms resulted in higher arapaima abundances, as it has been widely demonstrated to do in other studies of fisheries governance (Pomeroy and Williams, 1994; Berkes, 2007). Collective action arrangements resulting in the participation of all users affected by fishery rules is an important element of success in CBM schemes (Pollnac *et al.*, 2001; Pomeroy *et al.*, 2001). Aside from the importance of including all users as a means of supporting participation in the governing process as a whole, collective action arrangements benefit CBM by allowing local users to incorporate their knowledge of the resource system into the governance process (Berkes *et al.*, 2000; Cox *et al.*, 2010). Consistently, fairly, and objectively enforcing management rules

is an important element of success for fisheries CBM (Pomeroy *et al.*, 2001), as reflected by the presence of monitoring systems in the governance model for arapaima abundance. Participation by fishers in the monitoring programs creates a situation where guards are incentivized to prevent rule-breaking, as they directly benefit from the increased availability of the resource when rule-breaking is prevented. In tandem with monitoring systems, graduated sanctioning is an important component of fisheries governance. Consistently enforced penalties that are scaled to match the severity of rule-breaking instances are important for maintaining community cohesion while also appropriately punishing severe cases (Cox *et al.*, 2010).

It is critical to note that while our statistical and spatial analyses enabled us to create a comprehensive modeling assessment, the variables *not* selected for inclusion in the individual governance model may still play an important role. Minimum recognition of right to organize (I7) and nested enterprises (I8) were excluded from the statistical model because there was no variation in their measured values. However, right to organize (I7) and nested enterprises (I8) were both strongly present in all communities, and are an important precursor to the development of CBM governance. Similarly, defined boundaries (I1), congruence between rules and local conditions (I2), and collective action arrangements (I6) were excluded from the model, but their correlation with variables that were included in the model suggests that they function in concert with other mechanisms to promote successful governance.

The PCNM model was developed using a cutoff value of ~ 14.5 km (corresponding to the minimum distance needed to keep all sites connected). Further analysis of the spatial model revealed that contributions from the individual components, as well as total variation explained in the full partitioning model, could be influenced by altering the cutoff value in the PCNM calculations. Relative component contributions and total variation explained were stable at

values greater than the cutoff used. However, when the cutoff was reduced to a value that failed to keep all sites connected, individual contributions and total variation explained were sensitive to the particular value of the cutoff selected. Future work should explore the potential for spatial analysis across a range of scales to elucidate the changing contributions of human and environmental drivers to SES.

### *Conservation Implications*

Considered alone, any one of the three datasets could have provided reasonable explanatory power for managers attempting to understand the factors controlling arapaima abundance – particularly if additional variables had been introduced to further reduce the unexplained variation. A powerful spatial-only model would lend credence to the presence of underlying metapopulation dynamics effects, in which strong populations occur in spatially-clustered “hotspots”. Resultant management strategies would likely focus on the importance of individual populations in maintaining arapaima throughout the landscape. If only human effects were considered, the strength of the governance model would support the notion that governance is the primary factor controlling arapaima abundance, and as such, environmental effects might largely be ignored. Similarly, a landscape habitat-only model would likely support an ecosystem-based conservation approach instead of incorporating human influences. While any of the above strategies would not be entirely incorrect, they would be formulated upon an incomplete picture of the true factors controlling abundance. Given the results obtained by incorporating all three variable sets, arapaima management in this region would benefit from a multifaceted approach supporting the establishment of CBM schemes with specific rules, objectives, and monitoring programs in areas where CBM scores were low, while simultaneously promoting habitat

conservation and restoration in areas where important habitats (e.g., forests, shrubs, and macrophytes) have been reduced due to ranching and agriculture.

While the specific results from this study apply to arapaima in Lower Amazon floodplains, the methods used to obtain them should be generalizable to a variety of resource systems. The most obvious candidates for expansion of the techniques used here are other economically-important floodplain fish species, such as tambaqui (*Colossoma macropomum*), piracatinga (*Calophysus macropterus*), and surubim (*Pseudoplatystoma fasciatum*), among others. However, SES approaches are designed for use in a wide range of scenarios, and as such, the approach used here for arapaima could be easily modified to address questions outside of river floodplains or the tropics. By developing strong, independent models of human, environmental, and spatial effects, then linking them together using variation partitioning to understand the individual and joint contributions of each component, researchers may be able to pinpoint the drivers of resource abundance with much higher confidence than would result from traditional, singular approaches.

Understanding and incorporating the relationships between humans, the environment, and space in assessments of resource systems is essential for ensuring the long-term sustainability of natural resources. The strong overlap among habitat, governance, and spatial factors controlling the abundance arapaima in the study suggests that dispersal, source-sink effects, and metapopulation dynamics may act synergistically with governance and landscape habitat influences. Unravelling the specific mechanisms and connections operating within the observed overlap remains an important future research topic not only for arapaima, but also for many other resource systems. Human-environmental interactions can never be fully decoupled, therefore attempts to understand them should utilize a comprehensive approach that models them

simultaneously. Our results indicate that spatial analysis can serve as an effective mechanism to link and understand humans and the environment in social-ecological systems.

Table 2.1. Landscape habitat classifications, descriptions, and cost distance values (resistances) used to map connectivity of habitat patches potentially used by arapaima. N/A values occurred because the habitat classes underlying macrophyte beds were used in calculation of cost distances.

Dataset	Class Name	Average % of year flooded	Cost Distance	Description
Habitat classification	GrasslandHi	45	7.4	Grassland habitat (areas without significant tree or shrub cover), flooded only at high water
	GrasslandMid	62	6.2	Grassland habitat (areas without significant tree or shrub cover), flooded at mid water
	Forest	67	5.7	Seasonally-flooded forest areas
	Shrub	75	5	Shrub, short trees, or semi-shrub; includes aningais
	GrasslandLow	83	4.1	Grassland habitat (areas without significant tree or shrub cover), exposed only at very low water
	Floodplain Lake	100	1	Permanently flooded lakes and side channels (excluding main river channels)
	River Channels	100	1	Permanent mainstem river channel
Macrophyte presence	Never	N/A	N/A	Locations where macrophytes were never observed
	Irregular	N/A	N/A	Locations where macrophytes were present 1-3 out of 5 years
	Regular	N/A	N/A	Locations where macrophytes were observed 4-5 out of 5 years

Table 2.2. Variables, with formulae and descriptions, calculated for each class within the habitat and macrophyte data sets.

Dataset	Variable	Formula	Description
Habitat classification	Euclidean Nearest Neighbor, Area-Weighted Mean (ENNAM)	$NN = \sum_{j=1}^n \left[ h_{ij} \left( \frac{a_{ij}}{\sum_{j=1}^n a_{ij}} \right) \right]$	Average inter-patch distance between patches of the same type, calculated with a weight corresponding to patch size
	Class Area (CA)	$CA = \sum_{j=1}^n a_{ij} \left( \frac{1}{10,000} \right)$	Total area for a given patch type within the landscape
Macrophyte presence	Clumpiness Index (CLUMPY)	$CLUMPY = \frac{G_i - P_i}{P_i} \text{ for } G_i < P_i \text{ \& } P_i < 0.5, \text{ else } \frac{G_i - P_i}{1 - P_i}$	Measure of patch type aggregation based on cell-type (30 m x 30 m squares in the landscape) like-adjacencies (whether the neighboring cell is the same habitat or a different habitat classification) compared to a random distribution. Minimum value (- 1) for CLUMPY occurs when the patch type is maximally disaggregated, a value of 0 indicates a random distribution, and the maximum value (1) occurs when the patch type is maximally aggregated (i.e., completely contained within a single patch)
	Percentage of Landscape (PLAND)	$PLAND = \frac{\sum_{j=1}^n a_{ij}}{A} (100)$	Percentage area of each patch type in the landscape

Table 2.3. Variables (principles) and descriptions adapted from Arantes et al (2016), used to develop the Community-Based Management model relating governance principles to arapaima abundance at the community level. All continuous variables ranged from 0 (completely absent) to 1 (fully present).

<b>Principle</b>	<b>Name</b>	<b>Scale</b>	<b>Description</b>
11	Defined boundaries	Continuous	Clearly defined boundaries of the resource and its users
12	Congruence between rules and local conditions	Continuous	Rules of resource access and use (e.g. limits to gear, catch, areas, etc.) match local conditions
13	Collective action arrangements	Ordinal (Absent, Partially Present, Fully Present)	Functional collective action arrangements allow most individuals affected by the rules to participate in the definition and modification of the rules
14	Monitoring system	Continuous	Resource and behavior of the fishers is monitored
15	Graduated sanctioning	Ordinal (Absent, Partially Present, Fully Present)	Punishments for rule offenders based on severity and frequency of misconduct
16	Conflict resolution mechanisms	Continuous	Rapid and low-cost conflict resolution mechanism
17	Minimum recognition and right to organize	Continuous	Central governments formally authorize and recognize the rights of appropriators to devise their own institutions
18	Nested enterprises	Continuous	Nested structure of management tasks distributed across multiple levels and organizations

Table 2.4. Variables selected for each of the three independent models used in the variation partitioning analysis. Significant variables are denoted in bold. PCNM = Principal Coordinates of Neighbor Matrices. ENNAM = Euclidean Nearest Neighbor, Area-weighted Mean. CA = Cumulative Area. Brackets for governance variables indicate ordinal effect levels. Bold p-values are significant.

<b>Individual Model</b>	<b>Variable</b>	<b>Standardized Regression Coefficient</b>	<b>p-value</b>
Landscape habitat	ENNAM-Forest	-0.87	<b>&lt;0.0001</b>
	CLUMPY-IrrMacro	0.26	0.1045
	CLUMPY-RegMacro	0.35	<b>0.0106</b>
	CA-Lake	-0.50	<b>0.0003</b>
	CLUMPY-Shrub	0.88	<b>&lt;0.0001</b>
Governance	I3 [0.5-0]	0.65	<b>0.0390</b>
	I3 [1-0.5]	0.20	0.1974
	I4	0.31	<b>0.0344</b>
	I5 [0.5-0]	0.06	0.7412
	I5 [1-0.5]	0.56	<b>0.0075</b>
Spatial	PCNM1	0.36	<b>&lt;0.0001</b>
	PCNM2	0.33	<b>0.0023</b>
	PCNM3	0.06	0.6292
	PCNM4	-0.46	<b>0.0003</b>
	PCNM5	-0.34	<b>0.0031</b>
	PCNM6	-0.03	0.8467
	PCNM7	-0.59	<b>0.0008</b>
	PCNM8	0.21	0.2308
	PCNM9	0.04	0.8441
	PCNM10	-0.07	0.6762

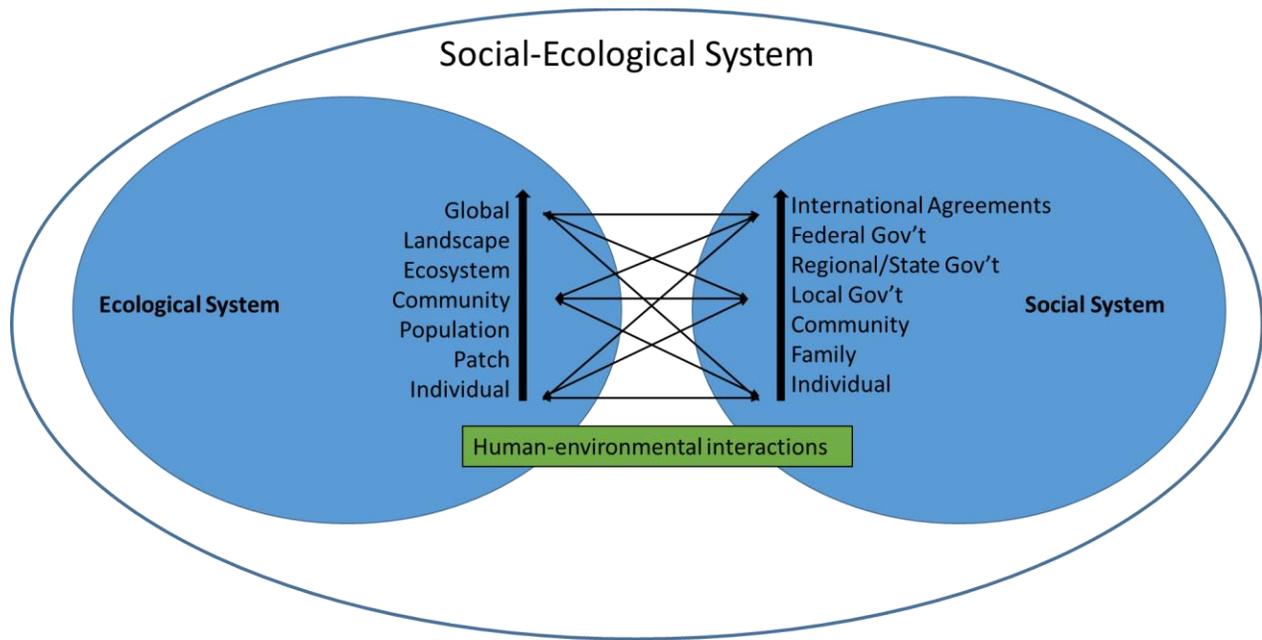


Figure 2.1. Conceptualization of the scales and interactions between social systems and ecosystems that collectively form a social-ecological system. Arrows indicate theoretical interactions between social and ecological systems that apply to a variety of contexts, though the importance and magnitude of these interactions requires data and modeling to depict for specific cases.

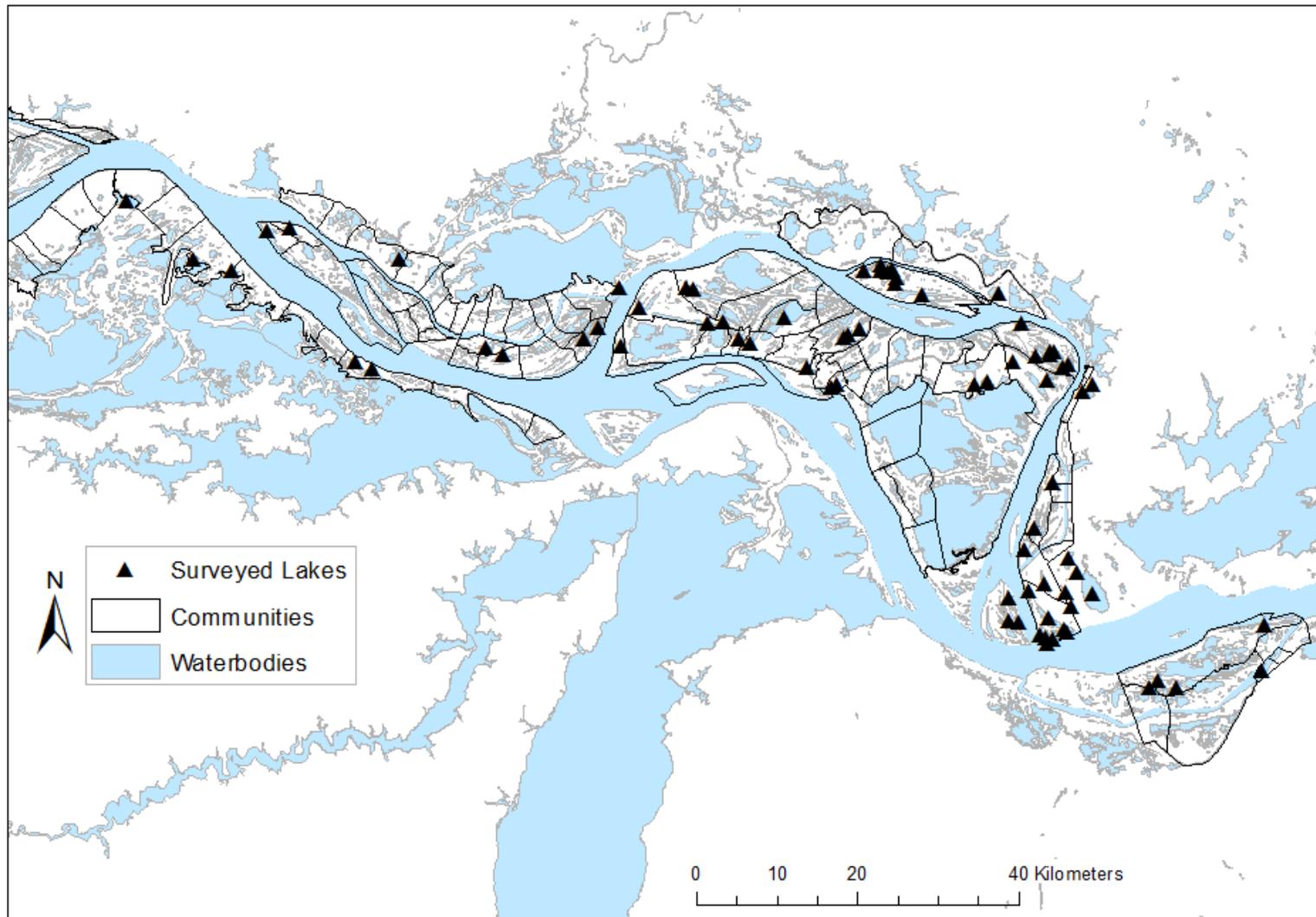


Figure 2.2. Map of the study system showing main river channels (dark blue), dry-season lake extent (light blue), fishing community boundaries, and lakes sampled (triangles).

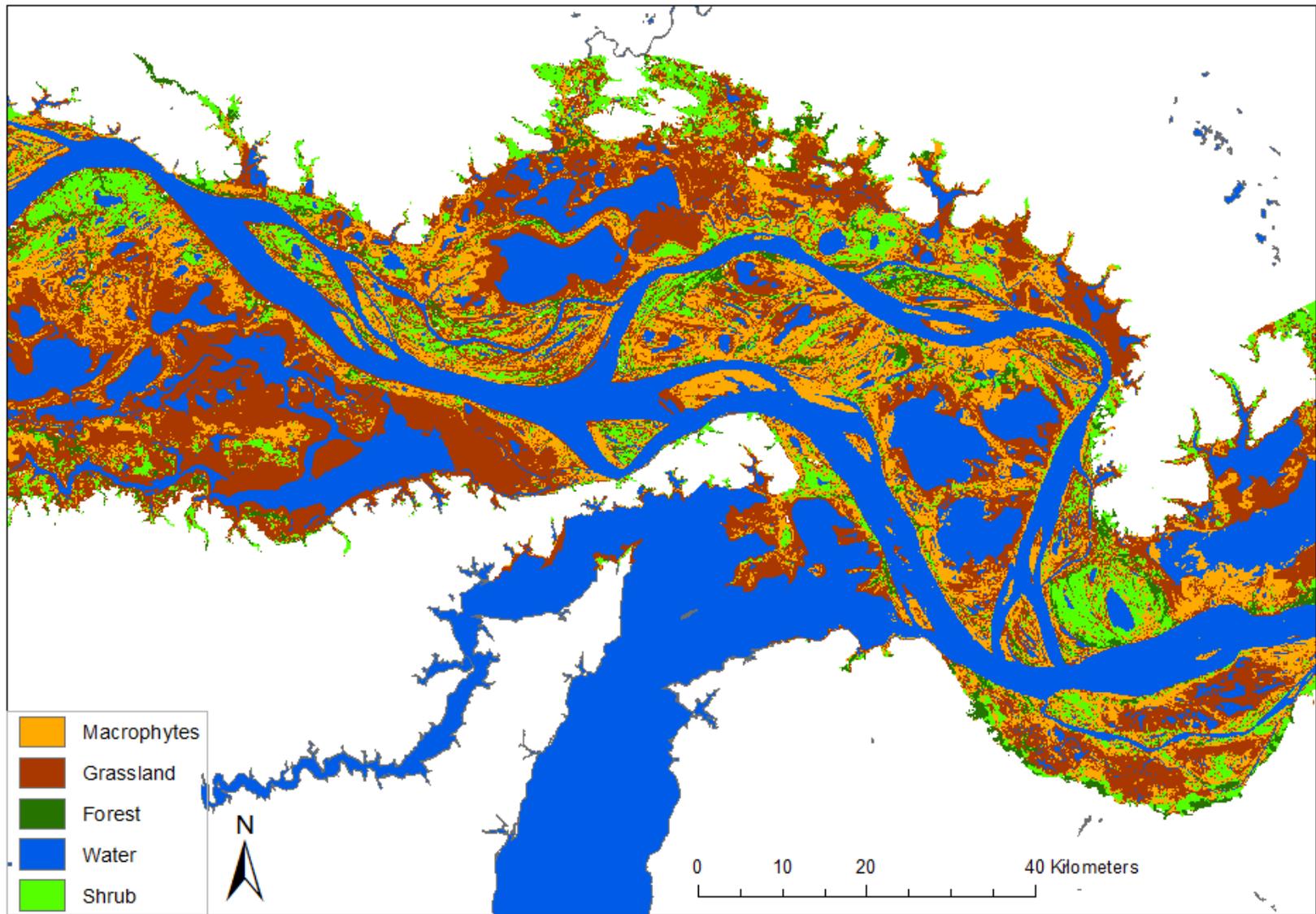


Figure 2.3. Map of habitat class coverage throughout the study area.

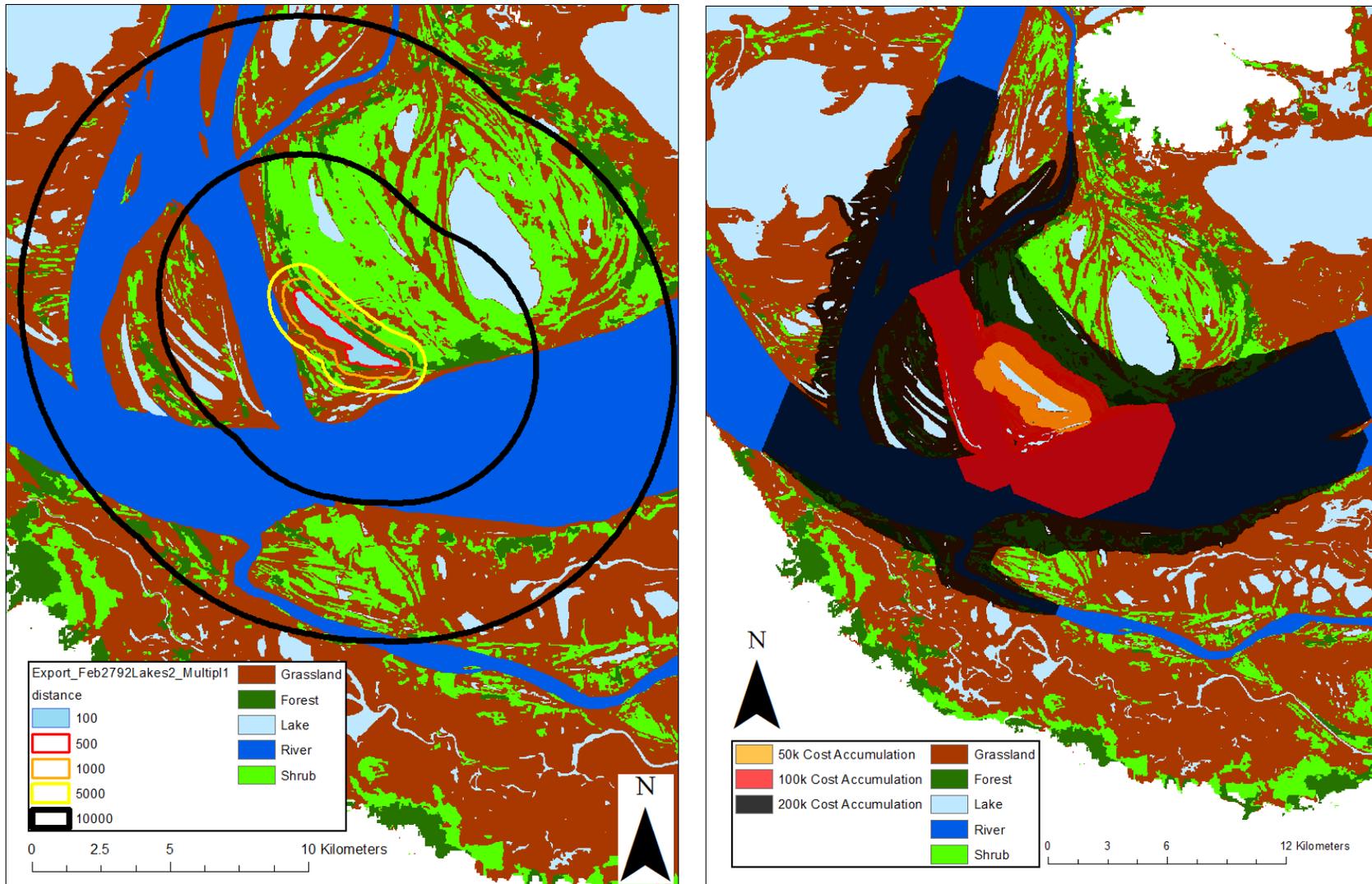


Figure 2.4. Comparison of traditional buffer-distance approaches to delineating available habitat surrounding a floodplain lake (left) with the cost-distance approach (right). By using the latter approach, dispersal of arapaima through potentially-available landscapes reflects patterns more consistent with true availability, based on the length of time each habitat type is available throughout the year.

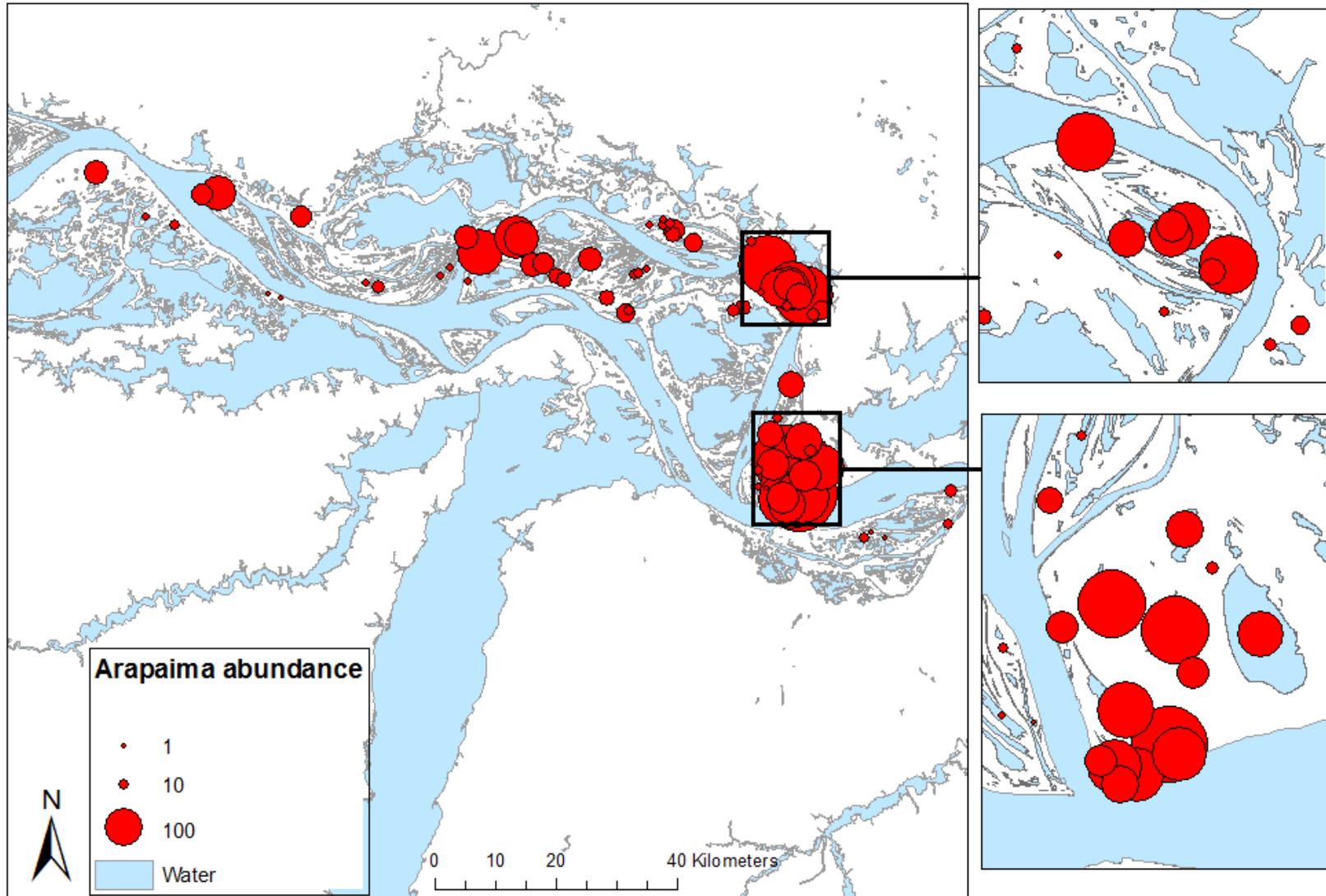


Figure 2.5. Map of arapaima abundances by study lake. Red circles are centered over each lake and scaled proportionally to the total number of arapaima counted in the lake. Inset maps show areas where numerous lakes were in close proximity.

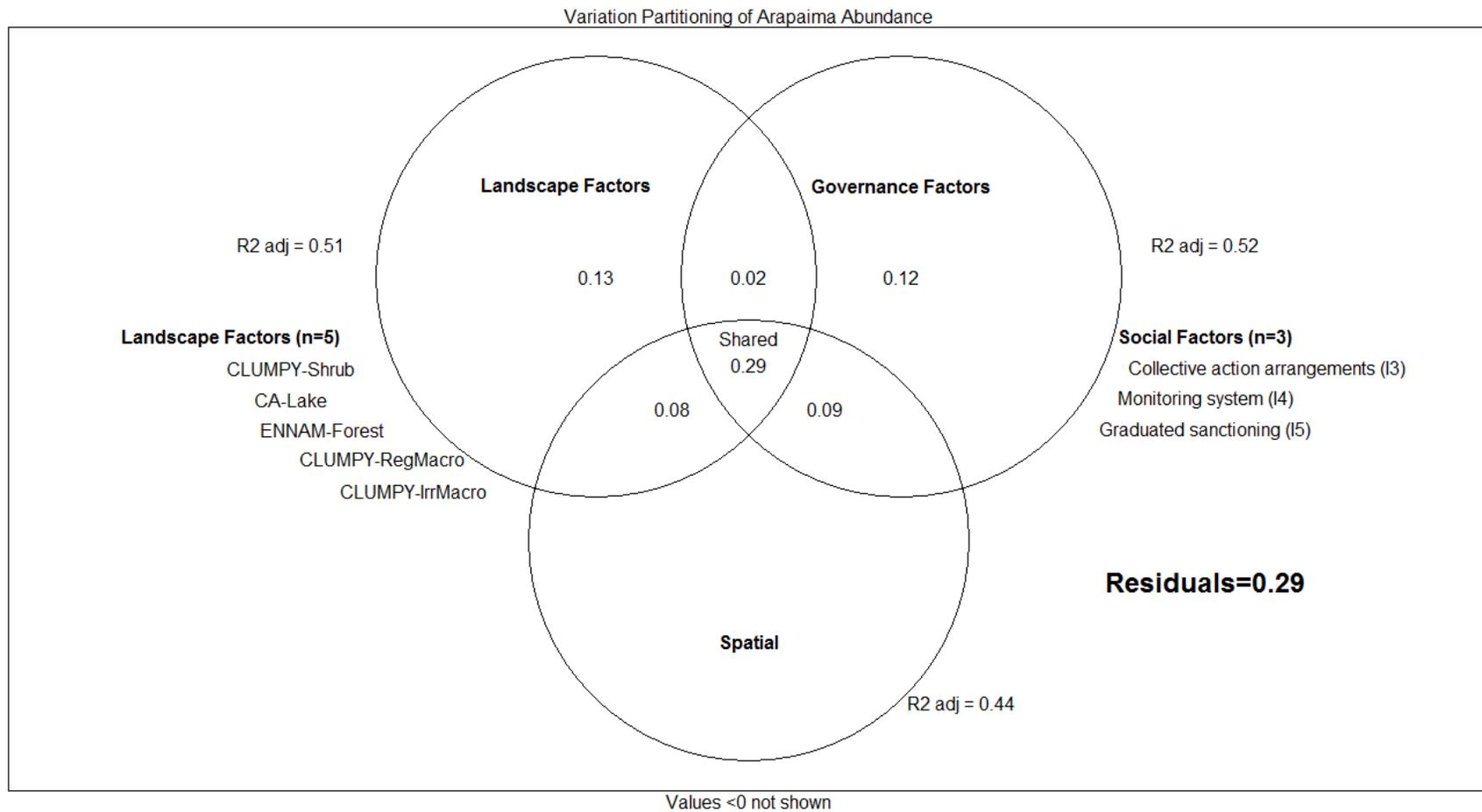


Figure 2.6. Venn diagram illustrating contributions of the three independent models in explaining the variation in inter-lake arapaima abundances.

## Conclusions

I think it is important to begin my thesis conclusions with an observation from my time working within the Amazon. In developing my thesis and working in the field, I came to treasure the information I obtained through anecdotes from researchers, conversations with fishermen, local knowledge, brief observations mentioned only in the conclusion sections of theses and dissertations, and other sources. As a whole, the value of knowledge I built from these sources was at least equal to that obtained from traditional scientific publications. With so much of Amazon fish ecology remaining unexplored and unpublished, I believe that collective observations, opinions, and instincts of researchers who have worked in the field are valuable resources that deserve publication in some form (though much of this information should be “taken with a grain of salt”). With that in mind, I have structured my thesis as two independent, publishable research articles, grounded in previously-published research and concluding only that which can be shown statistically. By contrast, these conclusions are an opportunity to discuss my findings for others in light of multiple lines of evidence, not just those that can be demonstrated with a p-value.

In the preface to this thesis, I described my hope that this research would contribute a potentially meaningful piece to the puzzles of both arapaima conservation and interdisciplinary fisheries conservation as a whole. With that goal in mind, I believe this work has yielded promising results in several ways, while also hinting at further processes for future investigation. Ecologically speaking, these studies have demonstrated that the floodplain habitats of the Amazon River play specific, important roles in supporting their native fish fauna. These fishes in turn support the human population by providing both food security and economic prosperity. In developing this study I found that both stage-structured habitat selection and dry season habitat

selection were largely unexplored topics for tropical floodplain fishes. Chapters 1 and 2 both provide new evidence of the important role of flooded vegetation (macrophytes, shrubs, and forests) for arapaima, and the habitat use patterns exhibited by small (< 1 m TL) arapaima suggest that these results are likely applicable to numerous other floodplain fishes. Further, the results reveal that depth plays a key role structuring the spatial distribution of arapaima within lakes during the dry season.

In my mind, chapter 1 demonstrates the kind of ecological research that focuses on a specific disciplinary concept (size-structured habitat selection) while also providing meaningful evidence to apply later to interdisciplinary investigations. As arapaima population monitoring and management continues to advance throughout the Amazon, knowledge of which habitats support arapaima at various life stages could become an important component for managing the population structures of local fisheries. Anecdotally, I was told by both fishermen and researchers that the youngest, smallest arapaima (< 0.5 m TL) are often found in very specific, secluded habitats with no larger arapaima present. These habitats are supposedly difficult to access, and often completely covered in “floating meadows” of dense macrophytes inaccessible to canoes. Despite my best efforts, I was able to find only a handful of these smallest individuals, and they were found alongside other, larger arapaima. From my experiences, I believe that these populations and habitats exist, and are important nurseries for recruiting arapaima to the age 1+ age class during their first dry season. Previous research and my own conversations with fishermen led me to believe that the majority of my “small” arapaima assessed in chapter 1 were individuals who would reach age 2 during the rising waters at the end of the dry season. That these age 1+ fish demonstrated distinct patterns of habitat selection – along with the possibility of age 0+ fish existing in distinct, unexplored habitats – suggests that size-structured habitat

selection by arapaima may be even more important than evidenced here. These possibilities make for excellent future research targets for fisheries studies throughout the Amazon.

The results from chapter 2 provide strong, fitting evidence supporting the notion that both human and environmental influences must be equally considered in integrated assessments of fish populations. The discovery that landscape habitats and local-scale human governance play almost equal roles in explaining inter-lake variability in arapaima abundances lends further credence to the growing body of literature supporting the necessity of interdisciplinary approaches to natural resources conservation. The importance of flooded vegetation habitats in particular spatial arrangements provides implications for future conservation strategies – namely that continued deforestation to support cattle ranching and further development may impair fisheries productivity.

One of the most tantalizing research targets resulting from my findings in chapter 2 is the unexplored migratory patterns of arapaima (and other floodplain fishes). Many fishes of the Amazon River exhibit extraordinary life history patterns involving complex migrations up the river timed with the flood pulse. Other less mobile fish (including arapaima) have been theorized to adapt their local-scale foraging movements to intercept yearly migration runs of prey species. Much of the evidence supporting these theorized movement patterns comes from unpublished data and conversations with fishermen, but it provides potential clues for future telemetry work. For arapaima, I am personally aware of two previous, three current, and several more future telemetry studies to document movement patterns across multiple scales of time and space. Despite having accessed results to four different studies (two of which occurred in the Santarém region), I am still at a loss to answer basic questions about arapaima movement ecology. The total range size, homing behavior (particularly repeated dry season lake homing), and migratory

nature of arapaima is largely a mystery. Understanding how, when, and why arapaima move has severe implications for pressing issues regarding arapaima. The future development of local-scale CBM, particularly in regions where arapaima populations are depleted, hinges on understanding the potential for arapaima to disperse (or not) from more concentrated populations. One of the critical components in developing the results from chapter 2 was the development of the connectivity analysis for floodplain lakes. I view this work as a promising way of understanding fish movement dynamics in floodplain systems, but the results would be greatly refined and strengthened with more explicit knowledge of the movement ecology of arapaima.

Oftentimes in the Amazon, the best way to obtain information about fish is to simply ask the fishers. My research experience in the Amazon mirrors that of many of my colleagues, in that reliable data collection often requires levels of effort orders of magnitude higher than similar studies in North America. Given the massive knowledge gaps in fish ecology throughout the Amazon, future studies may have promise in pairing ecological inquiry with traditional ecological knowledge (TEK). For example, if studies of fish movement in floodplain systems were paired with surveys of (TEK) from fishermen, we might be able to reliably gage the accuracy of easily-acquired information and begin subsequent telemetry studies with a much better idea of where and when to search for marked individuals. Similarly, my lakes yielding the lowest arapaima concentrations in chapter 1 occurred in areas where I was warned that looking for arapaima would be a borderline waste of time. I searched these lakes anyway, as I suspected that they might hold low concentrations due to the presence of some important environmental gradient, but the ability of fishermen to consistently predict where we could find arapaima is greater than that of any model I could ever develop.

My findings in this thesis continue to make it apparent that the biology, ecology, and sociology of fisheries are incredibly complex systems that can only be fully understood by developing a thorough understanding of each piece in the puzzle – and then putting all of the pieces together. The complexity of the individual pieces continues to grow, as my findings fall in line with other recent studies suggesting that simply understanding the habitat requirements of a species may not be enough. Just as ecological systems are constantly adapting and changing, individual fish face continuous shifts in their vulnerability to stressors, habitat needs, and prey selection. To ignore the significance of these often subtle, but important, shifts would be as detrimental as to consider conservation of fishes with no regard to human influences.

The interdisciplinary assessment developed in chapter 2 was an enormous undertaking that involved months of data collation, analysis, re-analysis, and development of new methodologies to link everything together. Defining “available habitat” in the constantly shifting floodplains to begin the landscape analysis was, by itself, a two-month process that took me hundreds of hours and dozens of failed models to develop. The end result – a completely new way of considering habitat connectivity that blends the spatial and temporal variation of the flood pulse – is presented in just two paragraphs of text in chapter two. Assembling the records for the arapaima count data and matching them to the lakes in our landscape database required help from dozens of individuals. Similarly, the governance variables included in the chapter 2 model were built by standing on the shoulders of our collaborators, who spent years conducting interviews on the ground and honing their understanding of which drivers within social systems to assess. Their data were condensed, analyzed, and fed into my modeling approach with only a brief outline of the work put into making them. This work was very much a team undertaking from the beginning, and the end results are far from perfect. For each question we have

(partially) answered, a dozen more have spawned, and it is already apparent to the authors involved how we can improve upon our work in numerous ways. However, I am hopeful that in presenting our work to the scientific community at large, we might help push knowledge of SES sustainability forward by some small increment.

To that end, my final conclusions from this work echo those from the very beginning: this thesis is but a small piece of the larger puzzle necessary to conserve the fish fauna of the world. I hope that, one day, someone will find at least some small part of it helpful.

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