Fishing and hunting in the Amazon floodplain: linkages among biodiversity conservation, rural livelihoods and food security

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DECLARATION

I hereby declare that this work has been originally produced by myself for this thesis and it has not been submitted for the award of a higher degree to any other institution. Inputs from co-authors are acknowledged throughout.

Daniel Tregidgo,

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'*Bicho*' Maya, it wasn't easy what we did: descend the River Purus twice, navigate 1000 km in a *rabetão* motorised canoe without knowing how, overwork until we grew boils, live together in the same (usually toilet-less) boat for half the year, and much much more. But with you I felt at home every day. You have a respect and such a strong connection with the people, that not just helped the research, but more importantly, left our friends from the Purus feeling happy for us to be there. Thank you for everything *meu bicho leso*.

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“*Biodiversity conservation is a luxury that human hunger overrides*”

Navjot Sodhi (the guy who got me into all this in the first place!), 2008

ABSTRACT

Billions of people rely on wild meat (wild fish and bushmeat) for their livelihood and food security, but unsustainable harvesting is causing pan-tropic defaunation. In addition to the decline of prey populations, many harvest-dependent societies in these regions are witnessing major social and environmental changes, including; rapid urbanisation, population growth, (unequal) socio-economic development, nutritional transitions, policy alterations, habitat conversion and climatic change. Despite the potential importance of these changes for biodiversity and human well-being, our understanding of how these changes are impacting the dynamics of harvesting systems is poor. In this thesis I engage with four major knowledge gaps, in particular. The first is that we know almost nothing about the relative influence of emergent large rainforest cities on wildlife. Second, the suggested connections between defaunation and food insecurity have weak empirical foundations. Third, links between aquatic and terrestrial ecosystems are largely neglected. And fourth, despite recent recognition of their importance, social-ecological feedbacks in tropical harvesting systems remain woefully understudied.

Hence, my overall aim in this thesis was to address these and related knowledge gaps by investigating the drivers and dynamics of contemporary wildlife harvesting in the Amazon, and assess the outcomes for biodiversity and rural food security. I focus on rural Amazonians, amongst who high levels of social marginalization, multi-dimensional poverty and food insecurity have been identified. These people are juxtaposed between traditional lives where seasons dictate subsistence wildlife harvesting, and a modern Amazonia in which rural livelihoods are increasingly influenced by the demands of growing urban areas, home to three out of four Amazonians. This PhD study was designed to capture the influences of the seasonal flood pulse and urban markets (metropolitan and provincial) in an extensive and largely-forested area of the Amazon floodplain. This was achieved by interviewing households in 22 communities during both the high and low water season along a 1,267 km stretch of the River Purus, the most important river for commercial fishing for Manaus, Amazonia's largest city of over 2 million people. Food insecurity was assessed during 556 household visits, in which time nearly 600 different harvesters were interviewed about their hunting and fishing activities, including detailed catch and effort data concerning 886 fishing trips.

I show that Manaus' favourite fish species (tambaqui, *Colossoma macropomum*) halves in body size and catch rate (catch-per-unit-effort in biomass; CPUEb) within several hundreds of kilometres of the city, with defaunation detectable 1000 km into the rainforest wilderness (Chapter 2). Despite defaunation of the main target species, rural fishers near to Manaus managed to maintain overall fish CPUEb, and levels of food insecurity were no worse than upstream (Chapter 3). Instead, I reveal severe seasonal food insecurity among the rural population associated with falls in aggregated fishing CPUEb of 73% during high waters. I provide novel evidence that food insecurity can result from significant falls in wildlife CPUEb (Chapter 3), and that this seasonal food insecurity may drive increased bushmeat offtake (Chapter 4). I also show in Chapter 4 how seasonal water-level and market forces can dictate wildlife harvesting profiles (akin to species assemblages). I provide evidence that the mechanism driving the defaunation seen in Chapter 1 and the differing harvest profiles in Chapter 4 is the regular service of city-based boats that purchase fish and deposit ice only in communities nearer to Manaus. Chapter 5 was inspired by listening to local voices, specifically, concerns that making a living is being increasing constrained by a combination of defaunation and environmental legislation. I explored these viewpoints using a social-ecological vulnerability framework, allowing me to better understand and voice their concerns, while contributing to the poorly studied concept of social-ecological feedbacks.

Through these findings, I establish and advance key links between drivers and dynamics of contemporary wildlife harvesting in the Amazon, and the outcomes for biodiversity and rural food security. As such, I emphasise the importance of taking a holistic view of the research and management of harvesting systems to help achieve sustainable food systems in the Amazon, and across the planet.

Key words: fishing, food security, hunting, interdisciplinarity, livelihoods

RESUMO EM PORTUGUÊS

Bilhões de pessoas dependem de carne selvagem (carne de caça e pesca) para seu sustento e segurança alimentar, mas a exploração insustentável está causando a defaunação nos trópicos. Além do declínio das populações de animais, as sociedades destas regiões que dependem da pesca e caça estão enfrentando uma rápida urbanização, crescimento populacional, desenvolvimento socioeconómico, transições nutricionais, alterações de

políticas públicas, conversão de habitats e mudanças climáticas. Apesar da potencial importância dessas mudanças para a biodiversidade e o bem-estar humano, nossa compreensão de como elas afetam a dinâmica dos sistemas de pesca e caça é escasso. Nesta tese englobo quatro grandes lacunas de conhecimento. A primeira é que não sabemos quase nada sobre a influência relativa das grandes cidades em florestas tropicais na vida selvagem. Segundo, as relações sugeridas entre defaunação e insegurança alimentar têm bases empíricas fracas. Terceiro, as conexões entre ecossistemas aquáticos e terrestres são geralmente negligenciadas. E quarto, apesar do reconhecimento recente de sua importância, os feedbacks sócio-ecológicos nos sistemas de pesca e caça tropical permanecem muito pouco estudados.

Assim, meu objetivo geral nesta tese foi abordar estas e outras lacunas de conhecimento, investigando as causas e dinâmicas da exploração contemporânea dos animais selvagens na Amazônia e as consequências para a biodiversidade bem como para segurança alimentar rural. Eu me foco no povo da Amazônia rural, onde se identificaram altos níveis de marginalização social, pobreza multi-dimensional e insegurança alimentar. Essas pessoas estão justapostas entre as vidas tradicionais, onde as estações ditam a pesca e a caça de subsistência, e uma Amazônia moderna em que os meios de subsistência rurais são cada vez mais influenciados pelas demandas de áreas urbanas crescentes, onde três quartos da população da região vive hoje. Este estudo foi projetado para capturar as influências do pulso de inundação sazonal e dos mercados urbanos em uma área altamente florestada na várzea da Amazônia. Isso foi atingido através de entrevistas em domicílios durante os períodos de cheia e seca ao longo de um trecho de 1.267 km do rio Purus. Este é o rio mais importante para a pesca comercial de Manaus, a maior cidade da Amazônia com mais de 2 milhões de habitantes. A segurança alimentar foi avaliada durante 556 visitas domiciliares, nas quais foram entrevistados cerca de 600 moradores sobre as suas atividades de pesca e caça, incluindo dados de captura e esforço relativos a 886 viagens de pesca.

Mostro que a espécie de peixe favorita de Manaus (*Colossoma macropomum*) diminui na metade o tamanho corporal e a taxa de captura (captura por unidade de esforço em biomassa, CPUEb) a centenas de quilômetros de Manaus, com defaunação detectável de mil quilometres da cidade (Capítulo 2). Apesar da defaunação da espécie-alvo, os pescadores rurais perto de Manaus conseguiram manter a CPUEb agregada dos peixes, e os níveis de insegurança alimentar não foram piores do que a montante (Capítulo 3). Em vez disso, revelo grave insegurança alimentar sazonal entre a população rural associada com quedas em

CPUEb de pesca agregada de 73% na cheia em comparação com a seca. Apresento novas evidências de que a insegurança alimentar pode resultar de quedas significativas na CPUEb dos animais selvagens (Capítulo 3), e que esta insegurança alimentar sazonal pode aumentar a caça (Capítulo 4). Também mostro no Capítulo 4 que o pulso da inundação e as forças do mercado podem ditar quais espécies serão pescadas e caçadas. Eu apresento evidências de que o mecanismo que causa à defaunação visto no Capítulo 1 e a variação nas espécies capturadas no Capítulo 4 é devido ao serviço de barcos da cidade que compram peixes e depositam gelo (recreios), que ocorrer regularmente somente em comunidades mais próximas de Manaus. O Capítulo 5 foi inspirado por ouvir as preocupações dos povos locais de que a vida está sendo cada vez mais restringida pela combinação da defaunação e legislação ambiental. Eu explorei esses pontos de vista usando uma estrutura de vulnerabilidade sócio-ecológica, permitindo-me entender melhor e expressar suas preocupações, ao mesmo tempo que contribuo para o conceito mal estudado de feedbacks sócio-ecológicos.

Através dessas descobertas, estabeleço e avanço conexões fundamentais entre as fatores reguladores e dinâmicas da pesca e caça contemporânea na Amazônia e as consequências para a biodiversidade e segurança alimentar rural. Como tal, eu enfatizo a importância de uma visão holística na pesquisa e gestão de pesca e caça para ajudar a alcançar sistemas sustentáveis de alimentos na Amazônia e em todo o planeta.

For Mum

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Chapter 1

GENERAL INTRODUCTION

Top: sunset over the River Purus, bottom left: gill-net fishing in an Amazonian lake, bottom-right: a hunted white-lipped peccary (*Tayassu pecari*). Photo credits: Daniel Tregidgo

This thesis engages with several of the so-called 'grand challenges' facing humanity and life on Earth. Ecosystems are suffering species losses at around a thousand times natural background rates (Pimm *et al.* 2014). In parallel, over a quarter of humans are suffering from malnutrition (Strang 2009; IFPRI 2016) as a result of food insecurity and ill-health. Biodiversity loss (Fig. 1.1) and food insecurity (Fig. 1.2) are therefore two of the most profound issues our planet faces (Rockström *et al.* 2009; Raworth 2012). The two issues are, however, intrinsically linked; most biodiversity loss stems from food production, which in turn (at least partly) relies on biodiversity (Sunderland 2011; Chappell & LaValle 2011).

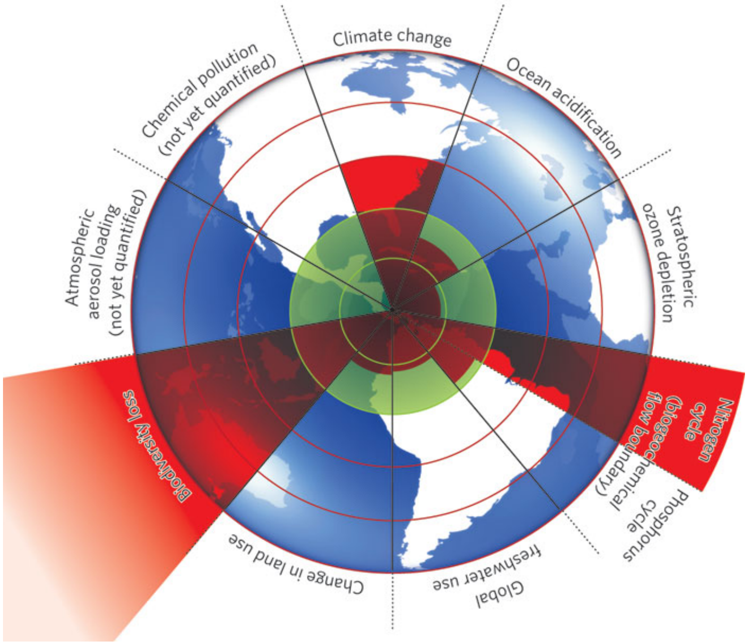

Fig. 1.1. Planetary boundaries. "The inner green shading represents the proposed safe operating space for nine planetary systems. The red wedges represent an estimate of the current position for each variable. The boundaries in three systems (rate of biodiversity loss, climate change and human interference with the nitrogen cycle), have already been exceeded." From Rockström *et al.* (2009)

Reliance on biodiversity is most direct where hunters and fishers harvest wild meats, in the form of bushmeat and wild fish. Hunting and fishing precede farming, yet the dynamics of harvester systems are changing dramatically in the modern world. This is true across the forested tropics, including in Amazonia, the world's largest rainforest and river basin. Here, the human population is growing, rapid urbanisation has resulted in 70% of residents living in urban areas (IBGE 2010a), human diets are shifting (de Jesus Silva *et al.* 2016), income sources are changing (e.g. Tepperman 2016), and climate change is increasing the frequency of extreme floods and droughts (Marengo & Espinoza 2016). At the same time overextraction of natural resources is devastating ecosystems (e.g. Peres *et al.* 2016), and legal legislation is responding by restricting extractive activities (e.g. de Almeida Corrêa, Kahn & Freitas 2014). Touching on all of these changes, this thesis aims to investigate the challenge of meeting the demand for animal protein at the lowest cost to Amazonian ecosystems. In this section ('General Introduction') I introduce the global issues of food security and biodiversity loss, examine the importance of bushmeat and fish for food security and livelihoods, review what we know about the biological impacts of hunting and fishing, and present the value of framing these issues in the context of social-ecological vulnerability. Finally, I give further context to the study system by describing relevant information concerning the Amazon, and outline the research objectives and structure of this thesis.

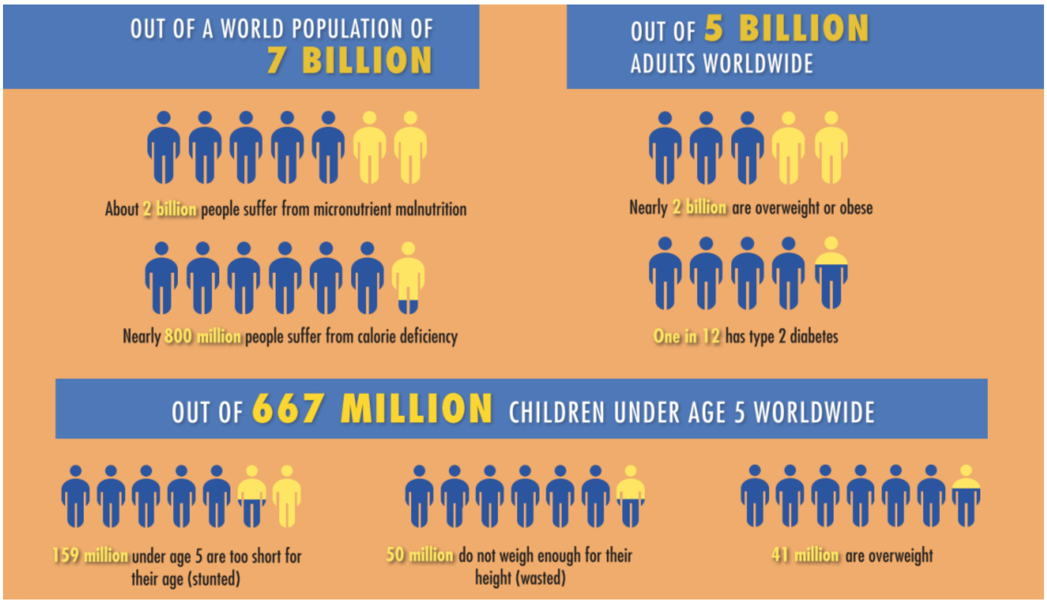

Fig. 1.2. The scale of malnutrition in 2016. Across the globe, one in nine people are undernourished (calorie deficient) (FAO, IFAD & WFP 2015), one in eight are obese (WHO 2015), and a quarter are micronutrient (mineral and vitamin) deficient (Strang 2009; IFPRI 2016). Together, these health problems are called malnutrition, which is caused by food insecurity and other food-unrelated factors. Figure adapted from IFPRI (2016).

1.1. Food security

Food insecurity affects around 2 billion people worldwide (Wheeler & von Braun 2013), and together with a combination of non-food factors, has resulted in widespread malnutrition. These non-food factors include poor sanitary conditions, water quality, and primary health care access, and a high prevalence of infectious diseases (Pinstrup-Andersen 2009). The extent of malnutrition remains serious, and worldwide, one in nine people (795 million) are undernourished (FAO, IFAD & WFP 2015), one in eight are obese (WHO 2015), and more than one in four (around 2 billion) are micronutrient (mineral and vitamin) deficient (Darnton-Hill *et al.* 2005; Strang 2009; IFPRI 2016).

1.1.1. Definition

Food security is defined as:

> "*a situation that exists when all people, at all times have physical, social and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life*" (FAO, IFAD & WFP 2015).

The definition encompasses four aspects: availability, access, utilisation, and stability (Schmidhuber & Tubiello 2007). Availability refers to our ability to produce enough food, and is often a main focus of efforts to solve food insecurity through increasing agricultural and fisheries production (Godfray *et al.* 2010; Béné *et al.* 2015). However, it is estimated that there is already enough food produced globally to feed everyone sufficiently (Banerjee & Duflo 2011), and therefore it is argued that that increasing food production is of little use while many cannot access it (Sen 1981). Although it is Important to note that even if food were distributed evenly amongst the global population, it is estimated that global food production would still need to increase (by almost 1000 calories per person per day) to feed an estimated global population of 9 billion people by 2050 (World Resources Institute 2013). Hence, increasing agricultural and fisheries productivity remains an essential element of food security (Godfray *et al.* 2010; Béné *et al.* 2015).

Access refers to the ability to acquire food. Sufficient food supply is often available, even where malnourishment is common, and therefore millions of people are not food-insecure due to insufficient food production, but due to poor global distribution and local accessibility. Food insecure households may live where there is enough food, but where they cannot afford it or lack the ability to obtain it (Arnold *et al.* 2011). Once food is accessed, utilisation refers to the need for sufficient food safety and nutrition, and therefore incorporates much more than just calorific value. Transitory (as opposed to chronic) food insecurity is that that occurs temporally (e.g. Ferro-luzzi *et al.* 2001), and stability refers to the need for food to be available, accessible and utilisable at all times.

1.1.2. Health implications of being food insecure

Food insecurity can have serious and often fatal health implications. This is particularly the case when suffered at critical life development stages, with pregnant women (Gernand *et al.*

2016) and children under 5 years (Bailey, West & Black 2015) at greatest risk, even to mild food insecurity (Schmeer & Piperata 2016). For example, it is estimated that undernutrition is a cause of nearly half (over 3 million) of all child deaths annually (Black *et al.* 2013). Wasting (a loss in bodyweight) or growth stunting are common symptoms of food insecurity (Black *et al.* 2008; Fig. 1.2), and can increase susceptibility to illness and disease, as well as cause irreparable damage to cognitive and physical function in children (Ferro-luzzi *et al.* 2001). However, as shocking as it is to know that in 2016 malnourishment is present in a quarter of the world's population, resulting in a half of all child deaths, it must also be made clear that the situation is improving. For example, 216 million less people are undernourished today than in the early 1990s (FAO, IFAD & WFP 2015).

1.1.3. Spatial patterns of food insecurity

There is significant spatial variation in food insecurity and malnutrition globally; largely that the problem is concentrated in developing countries (FAO, IFAD & WFP 2015; Fig. 1.3). For example, in Sub-Saharan Africa up to a quarter of the population are undernourished, while in South America this proportion has fallen from 15.1% in the early 1990s to under 5% today (FAO, IFAD & WFP 2015). However, inequalities are apparent on smaller scales, with large variation in food insecurity commonly witnessed between regions within countries (e.g. IBGE 2014), between households within the same communities (e.g. Harris-Fry *et al.* 2015), and even between people within households (e.g. women appear to suffer the most; FAO, IFAD & WFP 2015). Furthermore, rural people are generally considered to be at greater risk of food insecurity (FAO, IFAD & WFP 2015), although the urban poor are likely to be more impacted by price fluctuations (Rodriguez-Takeuchi & Imai 2013).

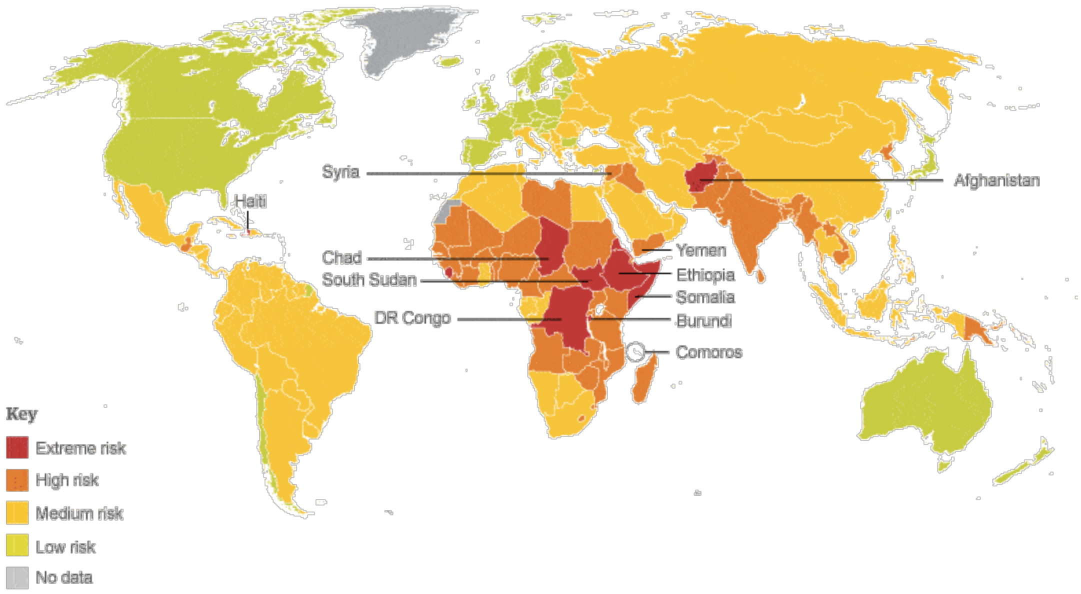

Fig. 1.3. A global map of food security risk. Note the greatest risk to food insecurity is in developing countries, and are generally located in the tropics (e.g. the Democratic Republic of Congo – home of one of the world's major rainforests), or are currently or recently in conflict (e.g. Afghanistan). The countries considered most at risk are labelled. Map made by Maplecroft (2013).

The most biodiverse areas of the world are those with the most threatened species, and the most malnourished and poor people (Mainka 2002; Fisher & Christopher 2007; WWF 2010; Barrett, Travis & Dasgupta 2011). In Fig. 1.3 note the high prevalence of food insecurity in the tropics, which harbour two-thirds of the Earth's species (Dirzo & Raven 2003). Moreover, Mainka (2002) estimate that around half the world's undernourished people live in the 12 'Megadiversity countries' identified by Mittermeier, Gil & Mittermeier (1997). Similarly, of the constituent countries that make up Conservation International's biodiversity hotspots (threatened areas with high endemism), Fisher & Christopher (2007) calculated that over a third of the national population were undernourished in twenty of them, and sixty percent or more were living below the poverty line in fifteen of them. Biodiversity conservation is a luxury that human hunger overrides (Sodhi 2008), and much of the biodiversity loss in these countries stem from food production (Geist & Lambin 2002). This was highlighted by the WWF (2010) who calculated that while the Earth's wildlife populations declined by 28% between 1970 and 2007, declines of 60% were seen in the tropics, and of 58% in lower income countries.

1.2. Biodiversity loss and implications for food security

The current global biodiversity crisis is facing the 'sixth mass extinction' (Barnosky *et al.* 2011; Fig. 1.1). Present species extinction rates are predicted at a thousand times the natural background rate (Pimm *et al.* 2014), and it is suggested by Primack & Ros (2002) that over 99% of current species extinctions are human induced. The proximate cause of most of these extinctions is probably food production, given that agriculture covers approximately 40% of the Earth's surface (Chappell & LaValle 2011), and overharvesting has defaunated many of our 'intact' ecosystems (Dirzo *et al.* 2014; Young *et al.* 2016). On land, tropical rainforests, which hold around half of Earth's species, are being lost at an historically unprecedented rate, equivalent to the area of around 50 football pitches a minute (Laurance 2010), largely as a result of agricultural expansion (Geist & Lambin 2002). In the oceans nearly 90% of fish stocks have been fully exploited or overexploited (FAO 2016) to feed humans directly, or indirectly via livestock (FAO 2016). And in freshwaters animal losses (defaunation) has been more severe than in marine or terrestrial realms (Jenkins 2003; Dudgeon *et al.* 2006; Young *et al.* 2016), yet the importance and impacts in these systems are underappreciated and poorly understood (Beard *et al.* 2011; Bartley *et al.* 2015).

Biodiversity is considered fundamental to human well-being (Naeem *et al.* 2016), and ecosystems provide a number of goods and services on which humans rely (Watson *et al.* 2005), including climate regulation, water purification, and food production. Evidence suggests that biodiversity is positively associated with several essential ecological functions that underpin agricultural food production, such as nutrient cycling, soil functions and pollination (Cardinale *et al.* 2012; Hooper *et al.* 2012). However, despite strong evidence that biodiversity loss is detrimental to human well-being in some places, evidence that this is true at a global scale is weak. Aggregate human well-being (including nutrition and food security) is increasing as ecosystem services degrade (Raudsepp-Hearne *et al.* 2010; Delgado & Marín 2016), and hence the cumulative food security implications of biodiversity loss are not clear.

Billions of natural resource users rely directly on biodiversity in the form of wild food, including wild fish (Golden 2016; Lynch *et al.* 2016) and bushmeat (Milner-Gulland & Bennett 2003; Cawthorn & Hoffman 2015), on which I will primarily be focussed in this thesis.

1.3. Wild meat and human well-being

Billions of people worldwide rely on fishing or hunting for their livelihoods and food security (Cawthorn & Hoffman 2015; Golden 2016; Lynch *et al.* 2016), the most reliant of whom are some of the planet's poorest and most vulnerable people (de Merode, Homewood & Cowlishaw 2003; Brown & Williams 2003; Béné 2009). These people commonly have few alternative sources of income and nutrition, thus making them highly sensitive to changes in wildlife populations (Golden *et al.* 2011; Golden 2016). Yet, wildlife harvest is a major contributor to pan-tropical defaunation due to unsustainable harvest levels (Milner-Gulland & Bennett 2003; Allan *et al.* 2005; Dirzo *et al.* 2014; McCauley *et al.* 2015; Ripple *et al.* 2016). The severe decline in the abundance of exploited species can threaten livelihoods and cause food insecurity by reducing the availability of protein, fat and micronutrients (Dirzo *et al.* 2014; McCauley *et al.* 2015).

1.3.1. Definition of wild meat

Much of the contents of this thesis concern the procurement (hunting, fishing, or collectively harvesting) and consumption of meat (animal tissue/flesh considered as food) from wildlife (any non-domesticated animals). In this thesis I define bushmeat (also known as game meat) as the meat from any wild (non-domesticated) terrestrial mammal, bird, reptile or amphibian (but notably not fish) hunted for food (Cawthorn & Hoffman 2015). I use the term wild meat to collectively refer to bushmeat and wild fish. This differs from some other work which use the terms bushmeat and wild meat interchangeably, not incorporating fish within the definition (Milner-Gulland & Bennett 2003). I do so because of the manner in which I emphasise the dual importance of bushmeat and fish for most individual harvesters, and the strong ties between wildlife harvest in aquatic and terrestrial systems.

1.3.2. Linkages between bushmeat consumption and human well-being

Bushmeat is fundamental to the food security and livelihoods of millions of people who rely on it for the majority of their protein, fat and/or income (Milner-Gulland & Bennett 2003; Cawthorn & Hoffman 2015). Those most dependent on bushmeat are often the poorest and most isolated people with few easily available alternatives (Robinson & Bennett 2002). Moreover it is clear that even where alternative meat sources are available, market prices very often determine food choices, and bushmeat is often a relatively cheap source of meat (Wilkie & Godoy 2001; Wilkie *et al.* 2005; Brashares *et al.* 2011). Even in situations where accessible alternatives to bushmeat exist, cultural tastes and preferences often exist towards bushmeat (Drury 2011; Brashares *et al.* 2011), which are extremely difficult to change, particularly when there is a lack of incentive to do so.

Very few studies have looked at the effects of bushmeat consumption, and therefore the impacts of terrestrial wildlife declines, on human health (Golden *et al.* 2011). Furthermore, most such studies discuss wildlife declines in the context of lack of protein, although bushmeat is also an essential source of fat (Sirén & Machoa 2008), and many other micronutrients and macronutrients (Sarti *et al.* 2015). Bushmeat provides much of the animal source foods consumed in many rural settings (Fa, Currie & Meeuwig 2003; Nasi *et al.* 2008). Animal source foods can provide a selection of micronutrients that are difficult to obtain enough of from plant foods alone (Murphy & Allen 2003). Research in villages in several developing countries identified six micronutrients (vitamin A, vitamin B-12, riboflavin, calcium, iron and zinc) to be particularly low in children with primarily vegan diets, even when protein intake appeared adequate (Calloway *et al.* 1992). The lack of these six micronutrients can cause anaemia, poor growth, rickets, impaired cognitive performance, blindness, neuromuscular deficits and eventually death. Animal source foods are particularly rich sources of all six of these nutrients, and relatively small amounts of these foods, added to a vegetarian diet, can substantially increase nutrient adequacy (Murphy & Allen 2003). For example, Golden *et al.* (2011) predicted that removing access from wildlife would triple the cases of anaemia among children in the poorest households studied. They predict that global declines in consumable wildlife, or access to it via conservation enforcement, could be detrimental to the health of wildlife-dependent populations.

1.3.3. Economic and cultural aspects of bushmeat consumption

People consume bushmeat for various cultural and economic reasons. Some people eat bushmeat because it is the only source of meat available, or hunt opportunistically. For example, people often hunt when venturing into the forest primarily for alternative purposes, such as logging (Tieguhong & Zwolinski 2009; Poulsen *et al.* 2009), oil extraction (Suárez *et al.* 2009) and the collection of non-timber forest products (Parry, Barlow & Peres 2009). Other people have a preference for the taste (e.g. Njiforti 1996), or because they enjoy the activity of hunting itself (Smith 2005). In some traditional cultures bushmeat has a ceremonial role in festivals (Adeola 1992; Sirén 2012), where in others, hunting is maintained by social norms and reinforced by gender interactions (Lowassa, Tadie & Fischer 2012).

The role of bushmeat in consumers' diets appears to depend on the relative price of other meats, and on wealth. Many people eat bushmeat because it is the most affordable meat available (Wilkie & Godoy 2001; Wilkie *et al.* 2005; Brashares *et al.* 2011). For example, a rise in bushmeat consumption has been demonstrated when the price of fish or beef increases

(Apaza *et al.* 2002; Brashares *et al.* 2004). Bushmeat can be an inferior good, meaning that poor people eat more than rich people, making it not a preference, but a necessity (Brashares *et al.* 2011). This is supported by evidence of price elasticity among wealthier households, that as income increases, consumption decreases, suggesting that they have other preferred sources of protein (Wilkie & Godoy 2001). On the contrary, bushmeat can also be a normal good, meaning that demand increases with wealth (Brashares *et al.* 2011), with bushmeat often taking a role as a luxury good (Drury 2011). Regionally, the role of bushmeat differs, and even within the same geographical region it can be an inferior good in rural areas and a normal good in urban areas (Brashares *et al.* 2011). This may be partially explained by the general trend for cheaper domestic meat closer to urban markets, and cheaper bushmeat closer to the location of capture (i.e. generally more remote rural areas) (Wilkie *et al.* 2005; Fa *et al.* 2009; Godoy *et al.* 2010; Brashares *et al.* 2011).

1.3.4. Linkages between fish consumption and human well-being

Humans livelihoods and diets are highly dependent on fish, which provides the global population with around 17% of its animal protein intake; rising to over 50% in many developing countries (FAO 2016). Additionally around a billion people rely on fish as their primary source of animal protein, particularly from poor rural communities in developing countries, many of whom have limited affordable alternatives (Kent 1997; Laurenti 2002; Allan *et al.* 2005). Worryingly, global marine fish catch has been falling by ~1% per year since around 1996 (FAO 2011; Pauly & Zeller 2016), leading to predictions that 19% of the world's population are vulnerable to nutrient deficiencies in the coming decades due to falls in marine catch rates (Golden 2016). However, in this thesis the focus is largely on freshwater fish.

Freshwater fisheries provide food for billions, and livelihoods for millions worldwide (Lynch *et al.* 2016), yet consumption and production data (Youn *et al.* 2014; Bartley *et al.* 2015; McIntyre, Reidy Liermann & Revenga 2016) and research on ecological impacts (Beard *et al.* 2011) lags well behind that of marine systems. In much of the developing world, freshwater fish are the main source of animal protein and micronutrients (including calcium, vitamin A, iron and zinc), because they are often the cheapest or only available source. Their importance for the poor is exemplified by the estimate that 95% of freshwater fish catches are from developing countries (Bartley *et al.* 2015). Freshwater fisheries are estimated to provide employment to 61 million people, 50% of whom are female (Bartley *et al.* 2015).

1.3.5. Wild meat as a safety net/coping strategy

While for some harvesters and consumers of wild meat it may not ordinarily play an important role in nutrition or income, it can act as an important safety net during shocks and lean seasons. A shock is an event that reduces well-being, such as illness, unemployment, drought, conflict, or agricultural price collapses (Marques 2003). Rural households are commonly faced with two types of shocks in tropical rainforests: idiosyncratic shocks that affect individuals or households such as illness or financial loss, and covariate shocks that affect groups of households, communities or regions, such as floods and fires (Coomes *et al.* 2010). Numerous idiosyncratic and covariate shocks can have profound effects on food security, for example through crop failures, loss of wild harvestable populations, loss of physical ability to undertake farming, hunting or fishing, or inability to afford sufficient food. Safety nets enable the poor to cope with shocks, thereby reducing their vulnerability (Dercon 2002). Natural ecosystems such as forests and rivers can act as safety nets for the most vulnerable during shocks (Coomes *et al.* 2010; Shackleton, Delang & Angelsen 2011). Many people may temporarily harvest natural products to meet emergency nutritional or financial needs when the primary resources (such as wild meat, medicines, or root crops) that support their livelihoods fail during shocks.

Some rural Amazonians cope with such shocks as illness (Ngwenya & Mosepele 2007; Coomes *et al.* 2010) and flood-induced crop losses (Takasaki, Barham & Coomes 2010; Coomes *et al.* 2010) by intensifying fishing effort. Ghanaian communities have been seen to increase hunting and bushmeat purchase to cope with overfishing-driven marine fish stock declines (Brashares *et al.* 2004). Local people in post-conflict Goma were found to be dependent on natural resources such as bushmeat due to a lack of other options (Ijang & Ndikumagenge 2013). Wittemyer (2011) found that elephant mortality and human-induced elephant wounding to be closely related with indices of local (but not national) economic conditions, suggesting that an economic downturn increases poaching for ivory and meat. In addition to acting as a safety net during shocks, bushmeat can help households fill seasonal or other cyclical food or income gaps. For example, in a community where bushmeat does not generally play an important role in nutrition, de Merode, Homewood & Cowlishaw (2004) observed a significant increase in the consumption of bushmeat and fish during the four month agricultural lean season, when the consumption and sale of agricultural produce reduced significantly. Similarly, an increase in bushmeat hunting effort and offtake (Endo, Peres & Haugaasen 2016), and bushmeat consumption (Poulsen *et al.* 2009) has been observed during high water seasonal falls in fish catch rate.

1.3.6. Substitutability between fish, bushmeat and domestic meat

The role of wild meats as safety nets/coping strategies can be viewed as positive from a human well-being perspective, but may have negative implications for environmental sustainability. Overhunting in tropical forests (Milner-Gulland & Bennett 2003), overfishing in aquatic systems (Pauly, Christensen & Guénette 2002; Allan *et al.* 2005), and agricultural land conversion (Chappell & LaValle 2011) are among the gravest threats to tropical biodiversity. However the issues associated with these different resource types have traditionally been treated completely separately, thereby not considering any resources linkages (Rowcliffe, Milner-Gulland & Cowlishaw 2005). Considering that few tropical rural people rely on a single resource to meet their protein needs, it seems sensible to assume that decreased availability or access to one such resource would increase demand for another. Bennett (2002) began the initial serious discussion of such substitutability between meat types, and some earlier studies demonstrate correlations between the price of one and the consumption of another (Apaza *et al.* 2002; Wilkie *et al.* 2005). Studies showing that consumers freely switch between bushmeat and fish are mounting (Table 1.1), with strong evidence for links between bushmeat consumption and national levels of fish production (Brashares *et al.* 2004). Assuming that human behaviour strongly links terrestrial and aquatic realms in this manner is a widespread phenomenon, research and policy should seriously consider the knock-on impacts of reduced availability of a resource via defaunation (Dirzo *et al.* 2014) or reduced access via restrictive environmental legislation. However, such connections between terrestrial and aquatic realms are still largely ignored in research and policy.

Table 1.1. Summary of linkages identified between bushmeat and fish harvesting systems

Reference	Factors affecting bushmeat	How it affects bushmeat	Location
Apaza *et al.* (2002)	Price of fish (and beef)	Price of fish (and beef) is positively related to with wildlife consumption	Bolivia
Loibooki *et al.* (2002)	Commercial fishing	Commercial fishing near Lake Victoria was linked to a decrease in bushmeat hunting (not quantified)	Serengeti, Tanzania
Brashares *et al.* (2004)	Fish stocks, price of fish, amount of fish sold in markets, and distance from coast	Overfishing reduces marine fish stocks, increases fish price, decreases amount of fish sold in market, and increases hunting in reserves. Relationships are stronger closer to the coast.	Ghana
Wilkie *et al.* (2005)	Fish consumption	More expensive bushmeat → less bushmeat consumption → more fish consumption	Gabon
Poulsen *et al.* (2009)	Fish availability	Less bushmeat consumed in dry season when fish was readily available	Northern Congo
Brooks *et al.* (2010)	Price of fish (and other alternatives)	Demand for snakes depends on the availability of alternative resources, mainly fish (principally for crocodile consumption)	Cambodia
Endo, Peres & Haugaasen (2016)	Fish catch rate	Bushmeat catch is higher when fish catch-per-unit-effort and catch is lower during the high water season	Brazilian Amazon

1.4. Biological impacts of wild meat harvesting

Even with their primitive weapons and relatively small populations, prehistoric humans hunted and fished numerous species to extinction. However with increasing human populations, improved access to diminishing habitats and advancement of harvesting tools, harvesting pressures on wildlife have greatly intensified in recent decades (Milner-Gulland & Bennett 2003; Allan *et al.* 2005; Roberts 2007; Young *et al.* 2016). The consumption of wild meat is resulting in widespread defaunation across terrestrial and aquatic ecosystems worldwide because exploited populations are widely harvested above the maximum sustainable yield (Milner-Gulland & Bennett 2003; Allan *et al.* 2005; Dirzo *et al.* 2014;

McCauley *et al.* 2015; Young *et al.* 2016). This decline in abundance of harvested species can cascade onto ecosystem functioning (Dirzo *et al.* 2014; McCauley *et al.* 2015; Young *et al.* 2016).

1.4.1. How much wild meat is harvested?

Estimates of bushmeat harvest vary widely, with published annual figures of 1-5 million tonnes in the Congo Basin (Wilkie & Carpenter 1999; Fa, Peres & Meeuwig 2002), 23,500 tonnes in the Malaysian state of Sarawak (Bennett 2002), and 67-165 thousand tonnes in the Brazilian Amazon (Peres 2000b). However these figures are only based on the data we have and we still have limited understanding of the volumes of bushmeat hunted and traded (Davies & Robinson 2007). For example it has been claimed that hunting in the Amazon is negligible due to the presence of large scale Amazonian beef production (Rushton *et al.* 2005; Nasi, Taber & Van Vliet 2011). However recent work in the Brazilian Amazon reports widespread wildlife harvesting even in remote areas (Parry *et al.* 2010b), in addition to 79% of urban households consuming bushmeat (Parry, Barlow & Pereira 2014). The authors suggest bushmeat hunting is vastly underestimated in the Amazon, and to warn of an Amazonian wild meat crisis. While accurate figures may be impossible to come by, it is generally accepted that offtake is higher in West-Central Africa than in Asia and South America.

Global marine fish yields have been declining ever since they peaked twenty years, while reported global catch in freshwaters continue to rise (Welcomme 2011; FAO 2016), having increased fourfold since 1950 (Allan *et al.* 2005). Reported yield from inland fisheries in 2008 was 10 million tonnes (FAO 2010), although real catches are thought to be much higher (Welcomme *et al.* 2010). This is because production and consumption data are scarce in freshwater systems (Youn *et al.* 2014; Bartley *et al.* 2015; McIntyre, Reidy Liermann & Revenga 2016). Catch and effort data are particularly difficult to obtain in small-scale tropical freshwater fisheries due to the high diversity of species exploited and gear used, variable fishing effort, diffuse landing sites, and often the remoteness of fishing sites (Hallwass *et al.* 2011). In fact while reported inland fish production is a fraction (under 14%) of reported marine fish production, Welcomme (2011) estimate that freshwater could rival marine production when all unassessed freshwater bodies (e.g. small streams, ponds, lakes and rivers) are accounted for (Fig. 1.4). This is incredible considering that freshwater makes up just 0.01% of the world's water, and 0.8% of the Earth's surface (Gleick 1996).

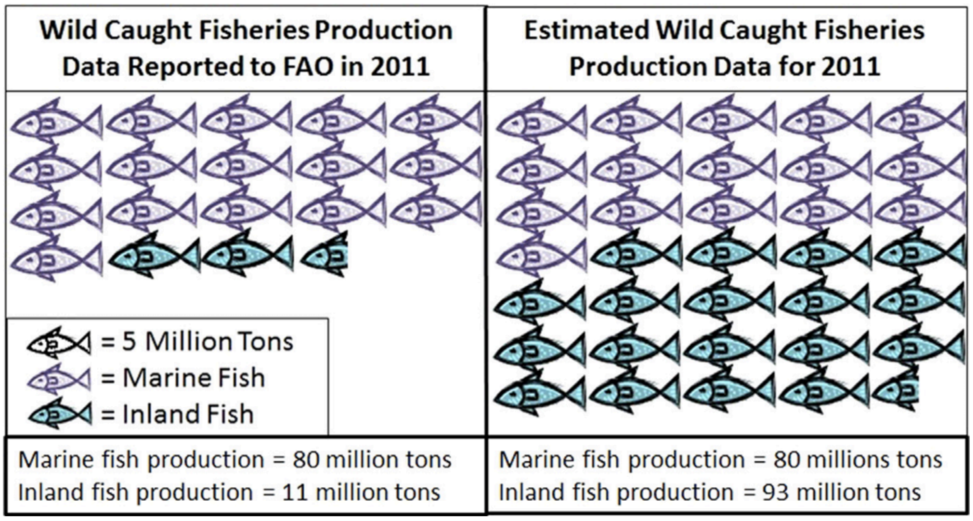

Fig. 1.4. Graphical depiction of reported and potential global fish production for marine and freshwater fisheries. Data from FAO (2012) and Welcomme (2011), and figure from Youn *et al.* (2014).

1.4.2. Biological impacts of bushmeat hunting

Tropical deforestation and degradation have been a major focus of academic study and conservation policy (e.g. REDD+; Saatchi *et al.* 2011) in the tropics, and together are thought to be the greatest threats to global biodiversity (Laurance & Bierregaard Jr. 1997), and to many essential ecological services that tropical forests provide (e.g. Saatchi *et al.* 2011). However, in stating that “we must not let a forest full of trees fool us into believing that all is well”, Redford (1992) emphasises the fact that much standing forest is depleted of its wildlife, with often profound knock-on consequences. It is thought that the majority of tropical protected forests are already considered empty, in that they lack all bird and mammal species over two kilograms, apart from a few hunting-tolerant species (Harrison 2011). Wilkie *et al.* (2011) state that hunting is the most serious threat to tropical mammals and birds after habitat loss. Furthermore, overhunting of tropical forests is a greater threat to biodiversity than deforestation in some regions, arguably a more immediate threat worldwide, and has long been considered the main cause of species depletion in otherwise undisturbed forest (Wilkie *et al.* 2011). Hunting also affects a considerably greater area of the tropical forest biome than deforestation and logging combined (Harrison *et al.* 2013).

Hunting leads to an obvious direct loss of animals (defaunation), and less obvious cascading changes in plant and animal community composition (Wilkie *et al.* 2011). Recent estimates suggest that at least 301 terrestrial mammal species are threatened with extinction as a result of hunting mainly for food and medicinal products (Ripple *et al.* 2016). Large-bodied vertebrates are depleted initially (Bodmer 1995; Peres 2000b; Jerozolimski & Peres 2003; Peres & Palacios 2007; Ripple *et al.* 2016), as they are targeted to maximise yield or gain social capital (Robinson 2000; Wilkie *et al.* 2011). In the absence of large animals, there is evidence of density compensation, whereby medium-bodied species (and maybe small-bodied species) become more abundant in the absence of large-bodied species by competitive release (Peres & Dolman 2000; Galetti *et al.* 2015). Multiple non-target taxa are directly or indirectly dependent on the most commonly hunted species'. Hence, cascading effects of hunting on multiple non-target taxa (including plants, insects and mammals) are caused by the reduction in wildlife diversity, reduction in total vertebrate biomass (Peres 2000a), and the selective defaunation of larger vertebrate species.

Hunting has been consistently shown to affect tropical forest plant communities by (1) reducing large seeds dispersed by bushmeat species, (2) reducing large seed predation by granivores (seed feeding animals), and (3) altering seed and sapling community composition (Stoner *et al.* 2007). These impacts are mainly due to the loss of heavily-hunted large-bodied animals, which are the principal dispersers and predators of many larger seeds (Poulsen *et al.* 2002; Dirzo, Mendoza & Ortíz 2007; Beckman & Muller-Landau 2007; Peres & Palacios 2007). Some studies even predict that this will lead to a loss of aboveground biomass and therefore carbon storage (Brodie & Gibbs 2009; Peres *et al.* 2016), as trees with denser wood tend to have larger seeds (Queenborough *et al.* 2009). Studies have found hunted forests dominated by plant species whose seeds are dispersed abiotically, or by smaller (non-hunted) animals (Nuñez-Iturri & Howe 2007; Terborgh *et al.* 2008). Furthermore the potential increase in small animals means that overall seed predation may increase (Dirzo, Mendoza & Ortíz 2007), potentially eventually inhibiting forest regeneration (Terborgh *et al.* 2001). Consequently, the overall effects of hunting on forests are thought to be negative, as large bushmeat species tend to be good dispersers, while small less-hunted animals tend to predate more on seeds.

Declines and losses of mammals as a result of hunting may impact on animals that indirectly depend on them. A reduction in the species richness and abundance of dung beetles in heavily hunted areas has been witnessed (Andresen & Laurance 2007; Nichols *et al.* 2009). Any such change in dung beetle community composition can have profound effects on the multiple ecological services that they provide, such as secondary seed dispersal and nutrient recycling (Nichols *et al.* 2008). There are also feedback effects of reduced tree generation back to larger-bodied species. As mature fruit trees die over time they are not being replaced in defaunated forests due to lack of seed dispersal, which means that these forests may become unsuitable for frugivores, who may not be able to find enough to eat. Effiom *et al.* (2013) found evidence of this, as three times as many primate groups and over twice as many fruit tree seedlings were observed in sites that were well protected from hunters.

1.4.3. Biological impacts of freshwater overfishing

Freshwaters may be the most endangered ecosystems in the world (Dudgeon *et al.* 2006), with species diversity declining faster (Jenkins 2003), and defaunation more severe (Young *et al.* 2016) than marine or terrestrial realms. Their fisheries are an essential and undervalued source of nutrition to billions, and livelihoods to millions of people worldwide (See section 1.4.1). Despite this, freshwaters are usually neglected in discussions of global fisheries, and there is a lack of research based understanding on the impacts of inland fisheries on ecosystems (Beard *et al.* 2011).

Freshwater overfishing mainly goes undetected (Allan *et al.* 2005) due to weak reporting (Bartley *et al.* 2015) and because declines take place within a complex of other pressures, such as water pollution and dam constriction (Dudgeon *et al.* 2006; Castello *et al.* 2013; Winemiller *et al.* 2016). Furthermore, total yields often remain high even in overfished freshwaters; in which certain species and the sustainability of the fishery are threatened (Allan *et al.* 2005; Fig. 1.5a). Overfishing in freshwater fisheries is instead characterised by the “fishing down” process, whereby more desired larger fish are initially depleted and eventually lost. There is also evidence that fishing pressure leads to an intraspecific reduction in fish size, whereby there is a reduction in the maximum length of an individual species within the fished population (Jørgensen *et al.* 2007). Hence, the main indicator of freshwater overfishing is a reduction of mean size (and age) of fish landed (Fig. 1.5b) (e.g. Castello *et al.* 2013), and the collapse of a particular species stock is a key symptom of intense fishing in inland waters.

Overall fishery production, and therefore total catch sustainability is rarely affected in overfished freshwaters. Catch often remains relatively constant over a large range of fishing pressure (Fig. 1.5a) as smaller species (which tend to be more biologically productive) replace larger species (which tend to be piscivorous), instead changing community structures (Allan *et al.* 2005; Welcomme *et al.* 2010). At the extremes, evidence supports the general model that there is an initial increase in catch as effort increases, followed by a steep decline in catch with sustained effort, thereby indicating a fisheries crash (Allan *et al.* 2005; Fig.

1.5a). In terms of livelihoods, heavy fishing in inland fisheries may not show changes in yields, but mainly reduces the abundance of desired species, reducing the value of the catch.

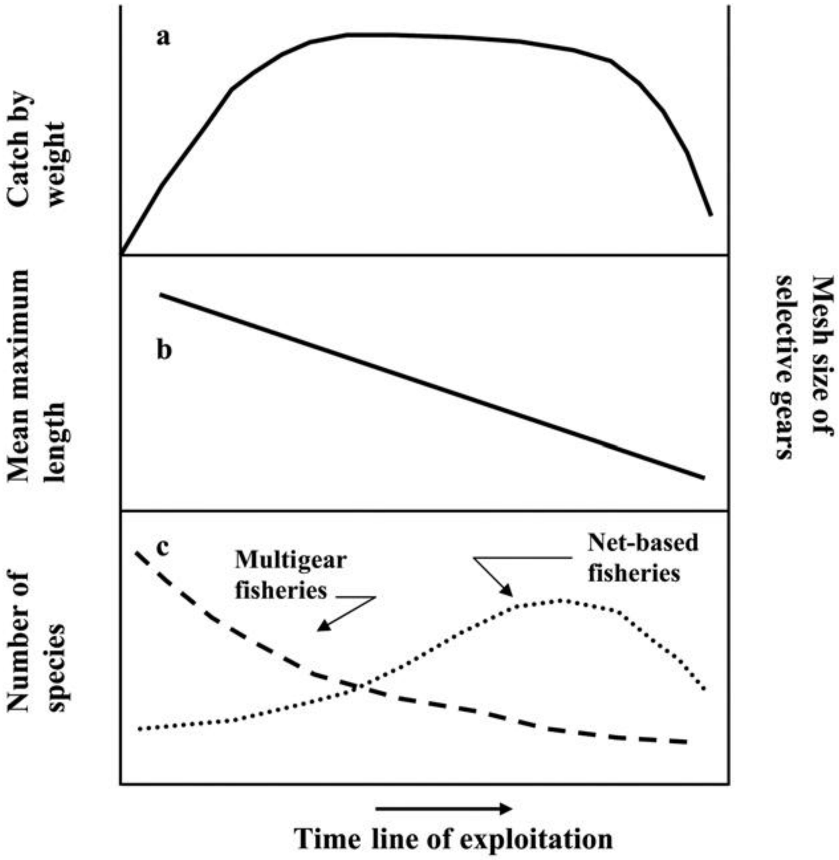

Fig. 1.5. Characteristics of fishing down in freshwaters. These include trends in various parameters of a multispecies fish assemblage in response to increasing effort: (a) total catch; (b) mean maximum length of assemblage and catch, and mesh size of nets; (c) number of species accessible to net-based and multigear fisheries. From (Allan *et al.* 2005)

The loss of large freshwater fish species or size classes can trigger ecological cascades. This is because they are often top apex predators with central roles in food web dynamics (Allan *et al.* 2005), or perform disproportionately important ecological functions, such as carbon flow modulation (Taylor, Flecker & Hall Jr 2006) and seed dispersal (Correa *et al.* 2015). Throughout Neotropical freshwater flooded ecosystems one of the main impacts of overfishing on ecosystem function is similar to that of overhunting: reduced seed dispersal. This is because many commercially important Neotropical fish species are frugivorous, and principally consume fruit during the seasonal flood period (Lucas 2008), thereby inadvertently dispersing seeds around the flooded forest. Some species are able to disperse seeds longer distances than almost any terrestrial seed disperser (Anderson *et al.* 2011).

Similar to terrestrial species, size matters, and larger-bodied fish individuals and species have been shown to be more effective seed dispersers, to disperse seeds from more plant species, and to disperse larger seeds (Anderson *et al.* 2011; Correa *et al.* 2015; Costa-Pereira & Galetti 2015). Hence overfishing-driven reductions in body size may impact plant communities in the flooded forest by inhibiting the ability of fish-dispersed seed species to germinate successfully, colonize unoccupied and distant patches and maintain gene flow across fragmented plant populations (Anderson, Rojas & Flecker 2009; Anderson *et al.* 2011; Correa *et al.* 2015).

1.5. Social-ecological vulnerability

The previous four sections (1.1 – 1-4) describe the vulnerability of people to livelihood and food insecurity, and of ecosystems to harm caused by over-harvesting animal populations. The term *vulnerability* can be applied to these cases, according to its common definition: the susceptibility to harm in response to exposure to a threat(s) (Rogers, Castree & Kitchin 2013). Additionally, the social-science concept of vulnerability is multi-dimensional and is a useful framework and heuristic tool for describing this state of human susceptibility to harm and guiding actions to reduce risk (Adger 2006). Moreover, studies are increasingly integrating social vulnerability to environmental change within multidisciplinary literature on linked (or coupled) social-ecological systems (Adger & Vincent 2005; Folke 2006; Gallopín 2006; Nelson, Adger & Brown 2007; Cinner *et al.* 2013b). This perspective can help us to understand the extent and importance of the links between social and ecological systems.

1.5.1. Social-ecological systems

Exploring the linkages between biodiversity conservation, rural livelihoods and food security in the Amazonian floodplain requires different kinds of knowledges stemming from both the natural and social sciences. Natural and social scientists now recognise that ecological and social systems should not be viewed in isolation (Milner-Gulland 2012; Ban *et al.* 2013; Castree *et al.* 2014; Fischer *et al.* 2015), yet disciplinary research endures. Natural scientists focus much of their effort on aiming to understand anthropogenic environmental impacts (e.g. Dirzo *et al.* 2014), and the effects of environmental change on human well-being has become a key focus across disciplines (e.g. Balmford & Bond 2005; Díaz et al. 2006; Adger 2000). Moreover, this research incorporates a growing understanding of how natural resource depletion can impact the well-being of people that are highly dependent on them (Pyhälä, Brown & Adger 2006; Allison *et al.* 2009; Golden *et al.* 2011; Golden 2016; Lam *et al.* 2016). As such, human and natural systems are increasingly being viewed together as linked or coupled social-ecological systems (Fischer *et al.* 2015). In fact, it has been argued that distinctions between the two are artificial (Hughes *et al.* 2005; Adger 2006).

1.5.2. Vulnerability

In exploring the linkages between biodiversity conservation, rural livelihoods and food security in the Amazonian floodplain, vulnerability can be a useful tool for describing the state of human susceptibility to harm and guiding actions to reduce risk. Vulnerability is defined as:

> "*the state of susceptibility to harm from exposure to stresses associated with environmental and social change and from the absence of capacity to adapt*" (Adger 2006).

The key parameters of vulnerability in Adger's (2006) framework are sensitivity, exposure and adaptive capacity. Sensitivity refers to the degree to which harm is likely to be experienced when exposed to a threat. As wild meat harvest provides an important source of income and nutrition to many people worldwide (Milner-Gulland & Bennett 2003; BNP 2009; Youn *et al.* 2014; FAO 2016), the livelihood and food security of these dependent people are highly sensitive to changes in wildlife populations (Allison *et al.* 2009; Béné 2009; Mills *et al.* 2011).

The impacts of change on sensitive social groups such as wild meat harvesters are co-determined by exposure to stresses and shocks that may limit their ability to make a living from wild meat. A harvester's ability to catch, transport or sell wildlife can be compromised by a range of factors including overharvesting, market fluctuations, and law enforcement (Cinner *et al.* 2011). Social-ecological vulnerability can occur in a harvesting system when human populations are dependent on exploiting natural resources that are themselves vulnerable (e.g. Golden 2016; Fig. 1.6). The ability of fishers and hunters to accommodate stresses such as resource-depletion by moving away from these constrained activities in order to successfully adopt alternative livelihoods is known as adaptive capacity (Adger 2006).

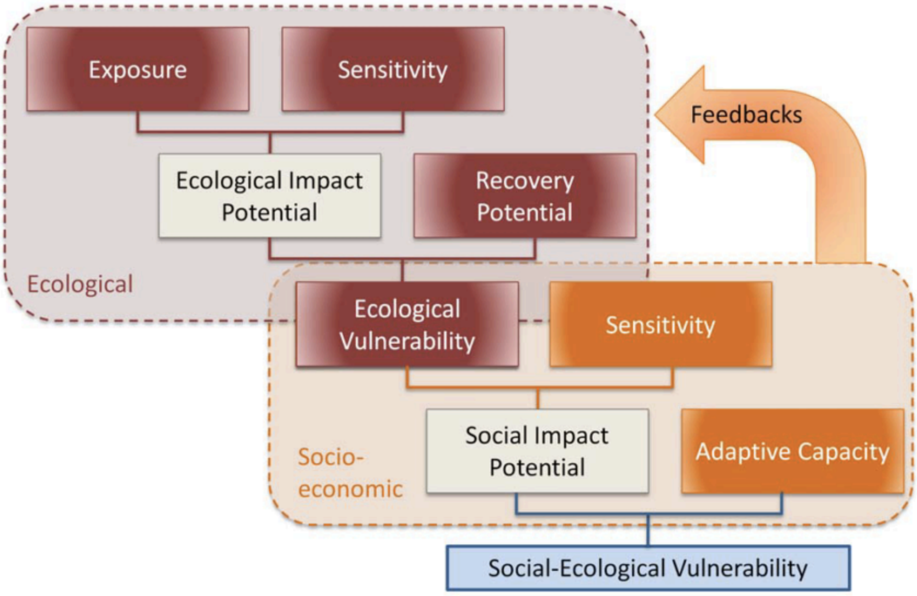

Fig. 1.6. Heuristic framework for linked social-ecological vulnerability. Taken from Cinner *et al.* (2013)

1.6. Study area

The Amazon basin (Fig. 1.7) covers 6.9 million km^2 (Goulding, Barthem & Ferreira 2003), containing over one million km^2 of freshwater ecosystems (Castello *et al.* 2013). The River Amazon alone is over 6,500 km long and discharges around 18% of global river discharge to the Atlantic Ocean (Meybeck & Ragu 1996). A quarter of all terrestrial species are found in the Amazon rainforest (Dirzo & Raven 2003), while its waters are home to far more species of fish than the Mekong and Congo basins combined (Winemiller *et al.* 2016).

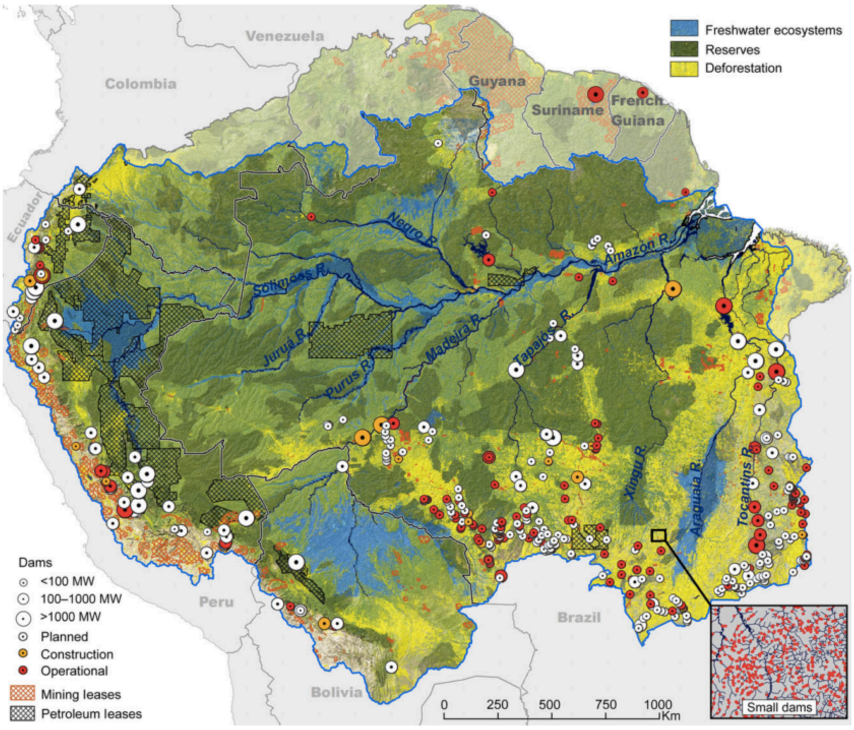

Fig. 1.7. Mapped threats to terrestrial and freshwater ecosystems in the Amazon. This map shows deforestation, dam construction, mining and petroleum extraction. Taken from Castello & Macedo (2016)

The threat to Amazonia that has received most international attention is deforestation (Fig. 1.7), which accelerated to unprecedented levels in the 1980s (Cardoso 2002). Since 2005, the annual rate of deforestation in the Brazilian Amazon has fallen by around 70%, despite population and economic growth in the Legal Amazon and the rest of Brazil (Nepstad *et al.* 2014). The principal threats to Amazonian freshwater ecosystems have been identified as deforestation, overfishing, dam construction, and pollution (Castello *et al.* 2013; Fig. 1.7).

The region has been considered a tropical wilderness area, given that a large proportion of the original vegetation is intact (particularly outside the 'arc of deforestation'), and that it has a low overall population density (Mittermeier *et al.* 1998). However, given that rapid urbanisation has occurred in recent decades, the region has been labelled as an "urbanised wilderness". In the Brazilian Amazon, where three quarters of the population lived in rural areas in 1950, three quarters - around 18 million people - now live in urban areas (IBGE 2010a). This enormous demographic shift brings profound opportunities (Aide & Grau 2004; Wright & Muller-Landau 2006) and challenges (Parry, Barlow & Pereira 2014) to humans and ecosystems, and adds an extra layer of complexity to the management and study of Amazonian human and ecological systems. While a large emphasis of this thesis concerns urban influences on people and ecosystems, our focal system is specifically the Amazonian floodplain social-ecological system.

1.6.1. The Amazonian flood pulse and floodplain

The seasonal flood pulse in Amazonia has an enormous impact on aquatic and terrestrial ecology (Junk, Bayley & Sparks 1989; Endo, Peres & Haugaasen 2016) and the activities of the local people in the floodplain (Harris 1998). The floodplain is inundated by a smooth and predictable flood curve with one pronounced peak per year. The flood pulse raises river levels by up to 15 m for as long as 6 months per year (Goulding, Barthem & Ferreira 2003). The mass of this water is so large that it is thought to be responsible for the greatest regular sinking in the Earth's crust (crustal oscillation) ever measured, at 50-75 mm (Bevis *et al.* 2005).

Fig. 1.8. The Amazon floodplain during the low water season. Everything up to, and slightly above, the level of the tree roots in the background will be annually submerged during the high water season. The beach in the foreground is covered in alluvial-rich sediment which originates from the Andes and is deposited each year during the high water season. Local people commonly plant crops here during the low water season, harvesting them before the floods inundate them. Photo credit: Daniel Tregidgo

The flood pulse connects the main channel to the abundant perennial lakes, and the floodplain forest (Fig. 1.9) helps to maintain diversity and productivity of fish (Castello, Isaac

& Thapa 2015). Many Amazonian fish species are migratory because the best breeding and feeding areas are in different places. Migration can be along the main channel (longitudinal) or from the main channel to the floodplains during high water (lateral) (Welcomme 1985). Lateral migratory fishes tend to be the most important for Amazonians, such as commercially important Arapaima (*Arapaima gigas*) and tambaqui (*Colossoma macropomum*) (Fernandes 1997; Castello 2008). Vegetated floodplains are important nursery habitats for fish larvae, thereby increasing survival rates. There is also an abundance of food here, permitting rapid growth.

Fig. 1.9. Fishing with a gillnet in the flooded forest during the high water season. Photo credit: Daniel Tregidgo

The people that live in the Amazonian floodplain are known as *ribeirinhos* or *caboclos*. They are Portuguese speaking peasants of mixed descent (indigenous Amazonian/European/African). *Ribeirinhos* are well adapted to the flood pulse (Harris 1998). Floodplain houses and other buildings are either built on stilts on the land, or on floating logs on the water (*flutuantes*) (Fig. 1.10). During the low water season when the fertile floodplain is exposed, they grow crops including manioc, beans and maize, while only those with access to permanently unflooded *terra firme* land are able to grow crops during the high water season. The high water season is also a time of less fisheries productivity, as fish are effectively diluted by the large volumes of flood water (Endo, Peres & Haugaasen 2016).

Fig. 1.10. A rural community in the floodplain made up of houses on stilts on the land, and floating houses (*flutuantes*) on the water. Photo credit: Daniel Tregidgo

1.6.2. Food security in the Amazon

Food security has improved dramatically in Brazil in recent decades, but extreme inequalities means that food insecurity remains an important issue for many Brazilians. The Brazilian Amazon suffers disproportionately more than much of the rest of the country, and in rural Amazonia food insecurity and malnutrition are common. Rural Amazonians have been shown to have high rates of child malnutrition, iron anaemia and vitamin A deficiency (Alencar *et al.* 2007, 2008; Piperata 2007; Piperata *et al.* 2013). Rural Amazonians are inherently vulnerable to food insecurity due to a combination of their socio-economic characteristics such as widespread poverty (IBGE 2010a), their remoteness (Maru *et al.* 2014), and their continuing reliance on wild protein and farmed calories (Murrieta & Dufour 2004; van Vliet *et al.* 2015a; Endo, Peres & Haugaasen 2016; Dufour *et al.* 2016), the availability of which fluctuate in time and space. Vulnerability to malnutrition is also high in rural areas as a result of poor sanitation (Piperata 2007), prevalence of parasitic insect-borne, water-borne and intestinal diseases, and poor access to healthcare.

Traditional foods such as fish and manioc dominate *ribeirinho* diets to this day (Murrieta & Dufour 2004; Fig. 1.11), but are being increasingly replaced by domestic meats and industrial and processed foods in what is known as a ‘nutrition transition’ (Sarti *et al.* 2015; van Vliet *et al.* 2015a; de Jesus Silva *et al.* 2016). In terms of animal protein, this largely includes cheap frozen chicken and processed meats (sausages and canned) (Nardoto *et al.* 2011; van Vliet *et al.* 2015a; de Jesus Silva *et al.* 2016). Relative to wild meats, these industrialised, processed and domestic meats are most prevalent in *ribeirinho* diets nearer to urban centres (van Vliet *et al.* 2015a). These foods tend to have a lower nutritional value than fresh fish and bushmeat (van Vliet *et al.* 2015a), and are thought to be contributing to forms of malnutrition previously not associated with poorer populations, such as obesity (Popkin & Gordon-Larsen 2004), which is now widespread in Amazonia (Alencar *et al.* 2007; Piperata 2007; Silva *et al.* 2016).

Fig. 1.11. A typical *ribeirinho* meal of fish and *farinha* (toasted manioc flour). Whether at work in the field (as shown here) or at home, these two ingredients remain present in almost every *ribeirinho* lunch and evening meal to this day. Together, they make up the vast majority of their protein and calorie intake (Murrieta & Dufour 2004). Photo credit: Daniel Tregidgo

Food insecurity health risks are exacerbated by non-food factors prevalent in the Amazonian floodplain, such as malaria (Katsuragawa *et al.* 2010) and iron-deficiency anaemia (Sarti *et al.* 2015). Malaria commonly becomes fatal by causing anaemia (Haldar & Mohandas 2009; Quintero *et al.* 2011). Additionally, poor sanitation in floodplain communities means that diarrhoea is commonplace (Piperata 2007), leading to the dietary loss of nutrients such as iron (Katona & Katona-Apte 2008). Some remote rainforest populations can obtain adequate protein from multiple dietary sources, while bio-available iron is only available from animal source foods (Beaton, Calloway & Murphy 1992; Neumann *et al.* 2003), and nutritional analysis suggests that dietary deficiencies leave Amazonians susceptible to anaemia (Sarti *et al.* 2015). Hence iron is a particular health concern in the Amazonian floodplain as a result of food and non-food factors.

1.6.3. Bushmeat harvest and consumption in Amazonia: the evidence-base

Hunting (Fig. 1.12) has been an important activity in the Amazon since ancient times (Shepard *et al.* 2012), and to this day bushmeat provides an important source of protein, fat and micronutrients to many Amazonians (Sarti *et al.* 2015; van Vliet *et al.* 2015a). Urban demand for bushmeat drives the "bushmeat crisis" in Africa (Bennett *et al.* 2007), but until recently it has been assumed that Amazonian urban bushmeat demand was "negligible" due to the large scale of livestock production in the region (Nasi, Taber & Van Vliet 2011). However, following recent evidence from two Amazonian cities that 79% of households consume bushmeat, Parry, Barlow & Pereira (2014) warn of Amazonian wild meat crisis. A series of papers in 2015 from the tri-frontier region of Amazonia between Brazil, Colombia and Peru support these claims (Sarti *et al.* 2015; van Vliet *et al.* 2015a; b).

Fig. 1.12. A paca (*Cuniculus paca*), recently shot the banks of the River Purus from this canoe. Today most terrestrial wildlife is hunted using shotguns, with hunting either undertaken on foot, or from canoes. Photo credit: Daniel Tregidgo

There is evidence of localised bushmeat species depletion as a result of overhunting (Peres & Nascimento 2006; Peres & Palacios 2007), and that bushmeat consumption in small urban centres may deplete commercially important bushmeat species over 100 km away (Parry & Peres 2015). Whereas aquatic species suffered basin-wide population collapse during the 20th century skin and fur trade, Antunes *et al.* (2016) suggest that many terrestrial species were spared due to the existence of extensive inaccessible forest 'refuges', which permitted population replenishment by source-sink dynamics. However, more areas are increasingly becoming accessible to hunters due the expansion of the road network in Amazonia, proximity to which appears to be associated with a reduced abundance of large-bodied target bushmeat species (Peres & Lake 2003).

1.6.4. Amazonian fisheries

Amazonian fisheries remain critically important to this day. Fisheries provide the principal protein source for *ribeirinhos* (Murrieta & Dufour 2004; Fonseca & Pezzuti 2013; Endo, Peres & Haugaasen 2016), a widespread essential livelihood activity, and important safety net (Coomes *et al.* 2010). Per capita fish consumption (Fig. 1.13) in the Brazilian Amazon is estimated at 94 kg/year in *ribeirinho* populations and 40 kg/year in urban populations, representing 5.8 and 2.5 times the world average respectively (Isaac & Almeida 2011).

Fig. 1.13. Cooking a typical catch from an Amazonian lake. Seen here are the popular food species cará açu *Astronotus* sp. (first on the left), curimatã *Prochilodus nigricans* (second on the left), tucunaré *Cichla monoculus* (fifth from the left), and aruanã *Osteoglossum bicirrhosum* (seventh from the left). Photo credit: Daniel Tregidgo

Commercial fishing is a lucrative business for some larger organisations, however the vast majority of fish sold commercially is caught by small-scale fishers. Most fish from wooden open canoes (6-8 m; Fig. 1.14) powered by paddling and/or an outboard engine (5-13 horse-power) known as a *rabeta*. They fish largely with gill nets, although depending on the target species, conditions and local customs, fishers also use a range of gears including tridents, harpoons, bow and arrow, hooks, fish traps and throw nets. For preservation some fish is salted, although nowadays most is now refrigerated in ice. Fishing enterprises will generally purchase from small-scale fishers, rather than employing labour (de Almeida Corrêa, Kahn & Freitas 2014). Many riverine community fishers fish largely to feed their families and local markets, but often sell high-value species to passing boats destined for cities (Junk, Soares & Bayley 2007). As well as subsistence and commercial fishing, ornamental fishing for aquarium fish and sport fishing is also important in some areas of Amazonia. However, ornamental and sport fishing supplies only minimal revenues to local communities, with declining demand and low prices for aquarium fish, and most profits from sport fishing going to large firms in Manaus or the United States (de Almeida Corrêa, Kahn & Freitas 2014).

Fig. 1.14. Catching the world's largest scaled freshwater fish species, arapaima (*Arapaima gigas*), with gill nets from a wooden canoe in an Amazonian lake. Gill nets are the most commonly used fishing gear these days, however many other gear are utilised depending on target species, conditions, and local customs. For example, a harpoon would usually also be carried on a trip like this targeting large arapaima individuals. Photo credit: Daniel Tregidgo

Global freshwater species richness and endemism is concentrated in Amazonia (Fig. 1.15). Almost 2,200 species of fish have been described in the Amazon basin (Albert, Petry & Reis 2011), around 200 of which are eaten by people, but only 6-12 make up over 80% of the landings in the large cities along the Amazon River (Barthem & Fabré 2004). This focussed pressure on few species has resulted in signs of overfishing in several species populations (Barthem & Petrere Júnior 1996; Isaac & Ruffino 1996; Batista 2000; Queiroz 2000; Petrere Júnior *et al.* 2005; Junk, Soares & Bayley 2007). Fig. 1.16 illustrates the resultant historical decline in mean body size of harvested Amazonian freshwater species. Harvests were dominated by Arapaima fish (*Arapaima* spp.), Amazonian manatee (*Trichechus inunguis*) and turtles (*Podocnemis* spp.) in 1895 (Veríssimo 1895), all of which are now considered endangered (Castello *et al.* 2013). Current fishery harvests are dominated by the endangered Arapaima, and the 17 species or species-groups labelled as "seemingly healthy" in Figure 1.16 (species 8-20) (Barthem & Goulding 2007). Hence, the mean maximum total length of fished species has reduced from 206cm in 1895 to 76cm today (Castello *et al.* 2013).

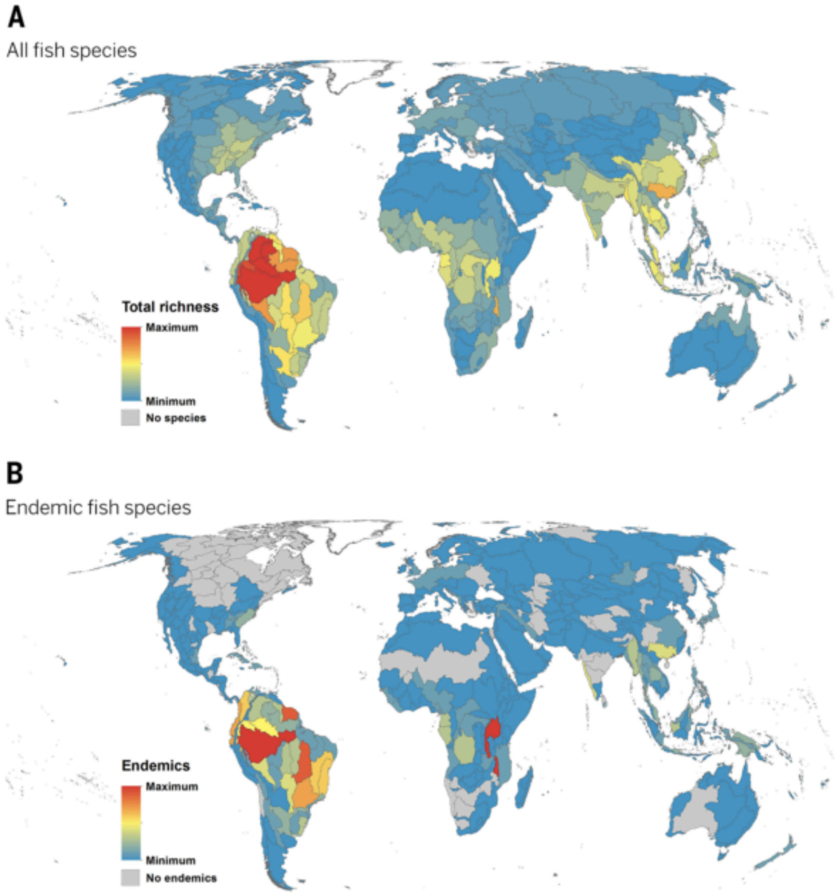

Fig. 1.15. Relative numbers of freshwater fish species in the different freshwater ecoregions. (A) All species and (B) endemic species. Maps from (Pimm *et al.* 2014) using data from (Abell *et al.* 2008).

Fisheries management throughout the Amazon is largely based on restrictions on when fish can be caught, the type of gear used, and the size and species of fish that can be sold (de Almeida Corrêa, Kahn & Freitas 2014), although community-based management approaches are becoming increasingly adopted (Petersen *et al.* 2016). For some threatened species, minimum size limits and closed fishing seasons during spawning seasons have been established to protect juveniles (de Almeida Corrêa, Kahn & Freitas 2014). In the 1970s and 1980s demand from urban populations and the export industry led to a rapid expansion of commercial fishing fleets, increasing competition and pressure on fish stocks (Almeida, Lorenzen & Mcgrath 2003). This resulted in widespread attempts by riverine communities to restrict commercial fishing in local floodplain lakes, although these efforts had no legal basis, and this led to conflicts (Mcgrath *et al.* 1993; Batista, Isaac & Viana 2004). Since 1998 Brazilian federal law has changed, allowing some of these fishing regulations on boat size, gear (commonly gill nets), and catch size created by local communities to be legally recognised and government enforced (Almeida, Lorenzen & Mcgrath 2002, 2003). The establishment of Reserves for Sustainable Development has been another approach to manage fisheries, sometimes giving the local population exclusive rights to exploit the natural resources (e.g. fish, timber and non-timber forest products). However, it is thought that increasingly common community co-management (Castello *et al.* 2009; Petersen *et al.* 2016) has seen the most success in fish management in the Amazon (Antunes *et al.* 2016).

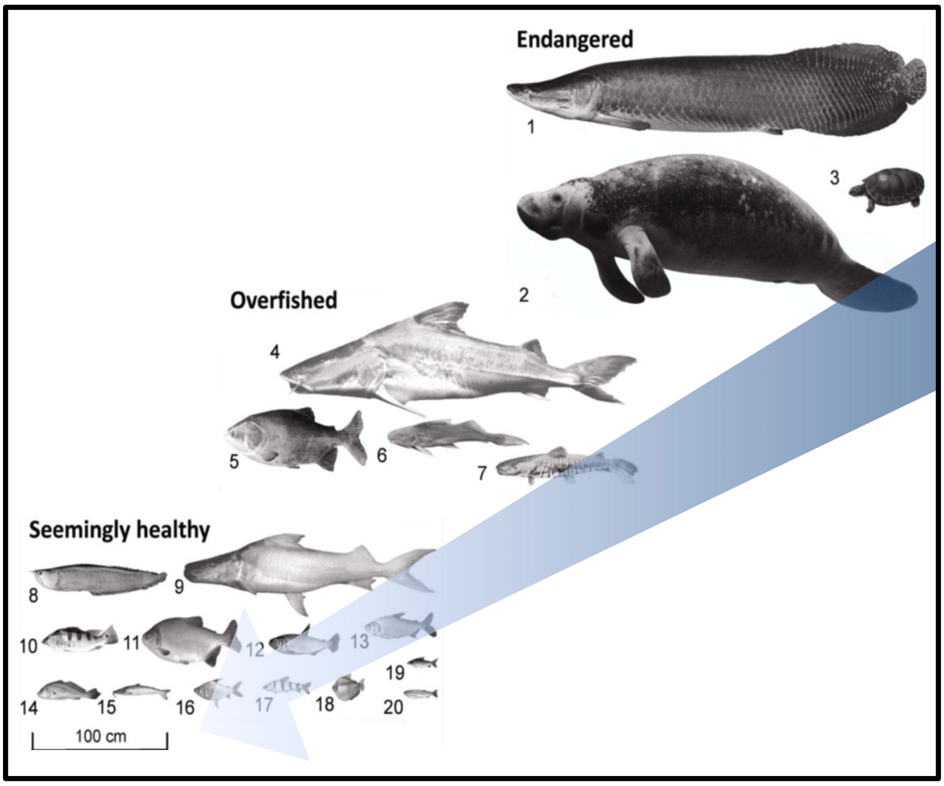

Fig. 1.16. Fishing down in the Amazon. Species or species-group codes are presented in parentheses, followed by the maximum body length of the species or mean maximum body length of the species-groups (from (Santos, Ferreira & Zuanon 2006; Barthem & Goulding 2007)), (1) 300 cm, *Arapaima* spp.; (2) 280 cm, *Trichechus inunguis*; (3) 40 cm, *Podocnemis* spp.; (4) 250 cm, *Brachyplatystoma filamentosum*; (5) 100 cm, *Colossoma macropomum*; (6) 100 cm, *Brachyplatystoma vaillantii*; (7) 100 cm, *Pseudoplatystoma* spp.; (8) 100 cm, *Osteoglossum bicirrhosum*; (9) 180 cm, *Brachyplatystoma roussseauxii*; (10) 55 cm, *Cichla* spp.; (11) 70 cm *Piaractus brachypomus*; (12) 50 cm, *Brycon* spp.; (13) 50 cm, *Prochilodus nigricans*; (14) 45 cm, *Plagioscion* spp.; (15) 40 cm, *Hypothalmus* spp.; (16) 35 cm, *Semaprochilodus* spp.; (17) 34 cm, *Schizodon* spp., *Leporinus* spp., *Rhytiodus* spp.; (18) 24 cm, *Mylossoma* spp., *Myleus* spp., *Metynnis* spp.; (19) 24 cm, *Curimata vittata*, *Potamorhina* spp.; (20) 22.5 cm, *Triportheus* spp. Adapted from Castello *et al.* (2013).

1.6.5. The River Purus

The study was carried out in rural communities in the floodplain along the mid-lower River Purus in the Brazilian Amazon (Fig. 1.17). The River Purus supplies more fish to the Amazon's largest city, Manaus (population 2.1 million people; IBGE, 2010), than any other river (Batista & Petrere Júnior 2003; Cardoso *et al.* 2004; Gandra 2010). However, apart from fishing pressure, the mid-lower Purus does not suffer significantly from the other major threats of Amazonian freshwater degradation: deforestation, pollution and dam construction (Castello *et al.* 2013). The mid-lower Purus River catchment meets the definition of a wilderness area (Mittermeier *et al.* 1998), with high remaining forest cover, and low human population densities (Table 1.2). It is the only major Amazonian tributary whose watershed remains undammed, and one of three with an undammed main channel (Winemiller *et al.* 2016). The River Purus sees some of the highest seasonal amplitudes (~15 meters) in river levels in the Amazon Basin (Castello & Macedo 2016), transforming much of the catchment into flooded forest.

Table 1.2. The study area (located entirely in the stated 4 municipalities) meets the definition of a tropical wilderness area, requiring it to be largely intact (>75% of original pristine vegetation remaining) and have a low human population density (<5 people/km^2) (Mittermeier *et al.* 1998). Percentage of intact original forest cover was calculated using data from the Brazilian National Institute for Space Research (Instituto Nacional de Pesquisas Espaciais (INPE) 2014), while population and municipality area data come from the 2010 Brazilian census (IBGE 2010a).

Municipality	% original forest cover	Population	Area (km^2)	Population density
Beruri	98.75	15,482	17,469	0.89
Canutama	96.57	12,733	33,643	0.38
Lábrea	94.81	37,505	68,263	0.58
Tapauá	99.64	19,047	84,946	0.22

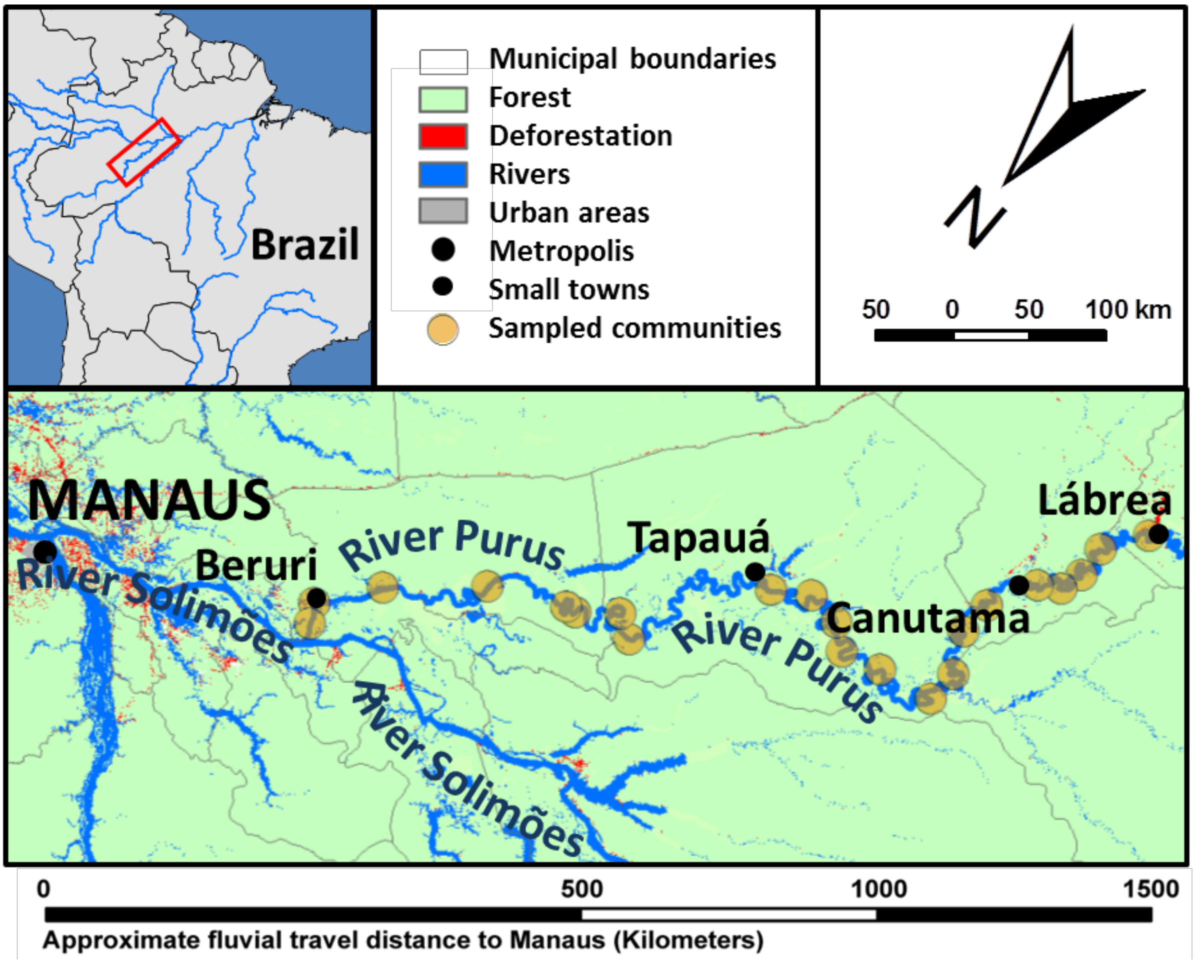

Fig. 1.17. Map of the River Purus. Urban settlements are found within municipalities, and take the same name.

1.7. Research objectives

The overarching objective of this thesis is to better understand the complex linkages between biodiversity conservation, rural livelihoods and food security in the Amazonian floodplain. Hence, this thesis engages with the challenge of sustainable food production. In aiming to achieve this I focus principally on fishing and hunting for wild meat, which is a principal revenue earner for many rural Amazonians, and remains an important source of protein for rural and urban Amazonians alike. This objective was addressed in the following four topics:

1.7.1. Chapter 2: Rainforest metropolis casts 1000 km defaunation shadow

Tropical forest regions worldwide are urbanising and developing rapidly, thereby changing the source and dynamics of demand for wild meat. However, most evidence for urban impacts on wildlife populations come from *ex-situ* market data, and the role of emerging metropolises in driving wildlife overharvesting is unknown. Therefore, the first research objective was to investigate the impact of Amazonia's largest city (Manaus) on a commercially and ecologically important fish species (tambaqui), and the knock-on consequences for the people and ecosystems that rely on it.

Chapter 2 research questions: (1) How far does the defaunation shadow of a rainforest metropolis extend into the forested wilderness? (2) Which factors determine the extent of this shadow? (3) What are the potential ecological and social consequences?

1.7.2. Chapter 3: Tough fishing in the flooded-forest: Severe seasonal food insecurity in a well-conserved region of Amazonia

We have very limited empirical evidence as to how changes in the relative and absolute abundance of wildlife populations may impact on the food security of human populations dependent on them. As such, we have poor ability to predict how different households will cope with widespread defaunation of wildlife that is occurring worldwide. The second research objective was therefore to investigate the presence and drivers of food insecurity among *ribeirinhos*.

Chapter 3 research questions: (1) How variable is the food insecurity of *ribeirinhos* in time and space? (2) Which kinds of rural households are most vulnerable to these spatial and seasonal-temporal constraints? (3) Is spatio-temporal variation in fish catch rate a proximate driver of food insecurity? (4) What responses do river-dwellers develop to low spatio-temporal fish catch rate?

1.7.3. Chapter 4: Exploring harvester vulnerability through analysis of fish and bushmeat catch composition

In investigating the human dimensions of wildlife population change, wildlife harvest is often seen in kilograms alone, and the importance of specific species to harvesters can be overlooked. This ignores the different importance of certain species to the livelihoods and nutrition of harvesters, and links between terrestrial and aquatic ecosystems. The third research objective was to explore how the fish and bushmeat catch of *ribeirinhos* might indicate their vulnerability.

Chapter 4 research questions: (1) How do spatial, temporal and landscape factors determine fish and bushmeat catch composition in this harvesting system? (2) Which taxa contribute most to dissimilarities observed in time and space? (3) Are there changes in the biomass of bushmeat hunted per household which can be associated with fish catch rates?

1.7.4. *Chapter 5: "Everything we do is illegal": complex linkages between vulnerable natural resource users, their environment, and environmental legislation*

Wildlife harvesters depend on the state of wildlife populations and their legal rights to harvest and sell their catch to make a living legally, and hence defaunation and ensuing restrictive legislation will likely constrain their livelihoods. A harvester that is vulnerable to such constraints on the harvest of important species may adapt by switching their efforts to other, potentially sensitive, species. The final research objective was to explore how defaunation and environmental legislation is constraining *ribeirinho* livelihoods, and potentially indirectly increasing pressure on wildlife.

Chapter 5 research questions: (1) How have residents of the resource-rich Amazonian floodplain become fisheries-dependent? (2) How are changing social-ecological systems constraining fishery-derived livelihoods? (3) How may livelihood vulnerability feedbacks impact ecological vulnerability?

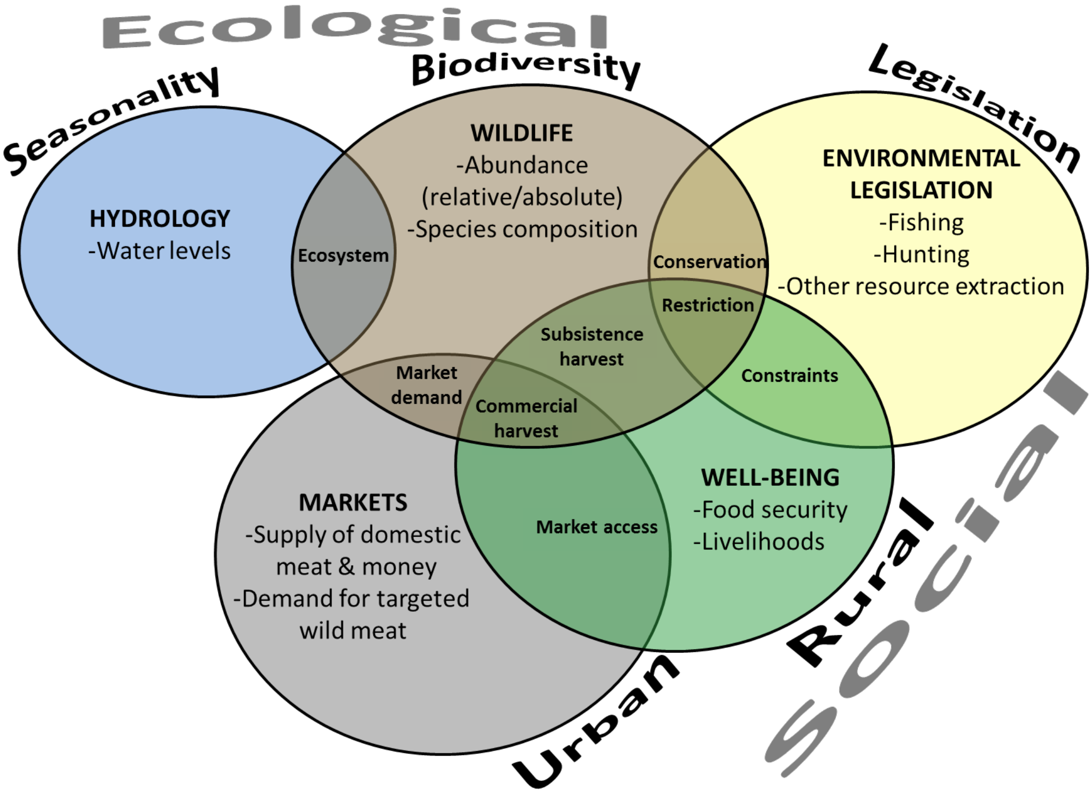

Fig. 1.18. Conceptual diagram of the key facets (bubbles) of the social-ecological system under study in this thesis. The key features of interest of each facet are the bold-capitalised headings inside each bubble, followed by bullet-pointed indications of each feature. Through these connections I suggest that seasonality, urban markets and legislation have key direct or indirect influences on biodiversity and rural well-being.

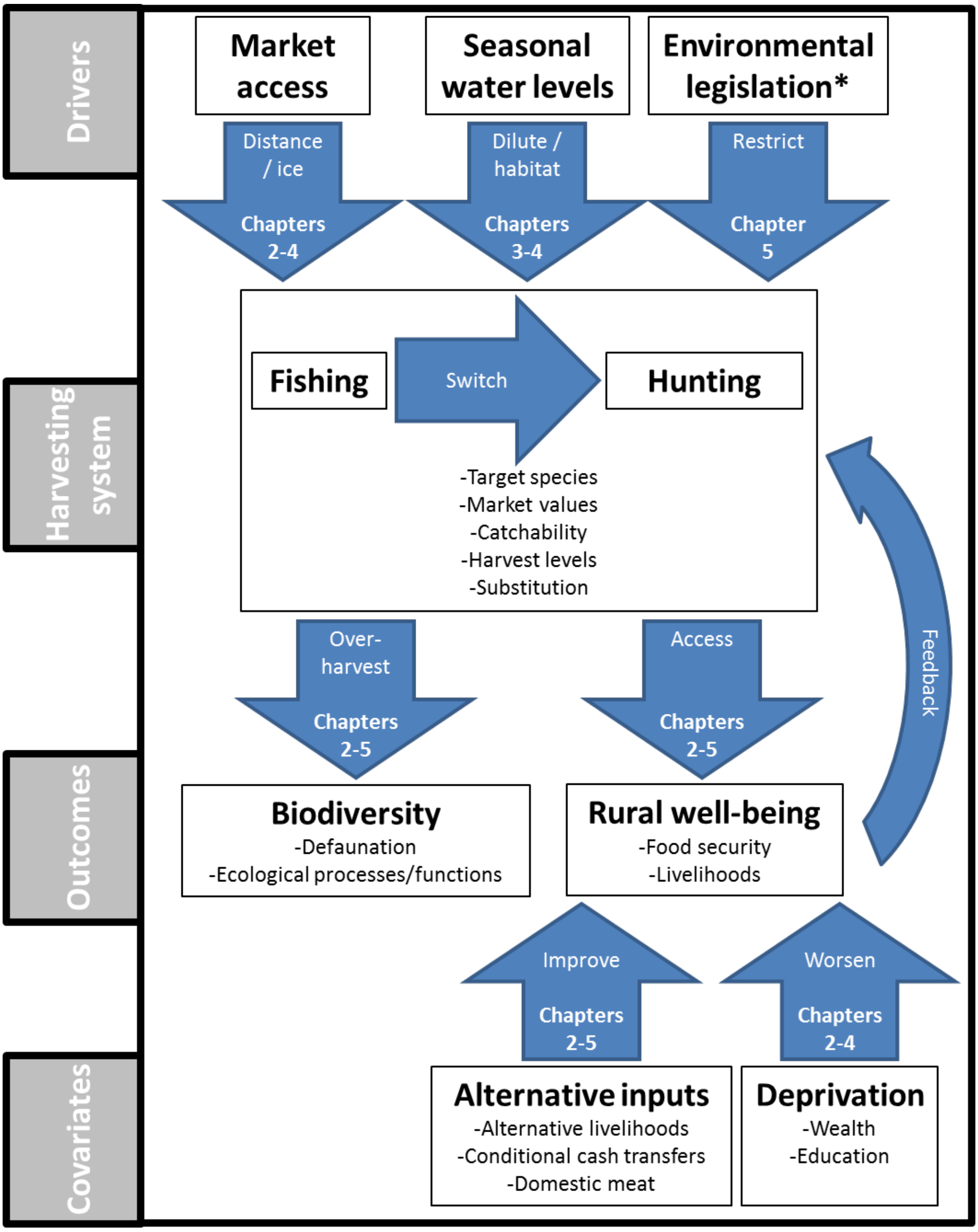

Fig. 1.19. Conceptual diagram of the proposed connections (arrows) between the focal drivers, harvesting system, outcomes and covariates (boxes). The chapters which specifically address these issues are identifies within the arrows. *Note, this thesis did not originally focus on environmental legislation as a key driver of the harvesting system dynamics that in turn influence outcomes, however its importance became apparent through deductive reasoning.

1.8. Thesis structure

Each of the data chapters of this thesis has been written for publication: at the time of submission, Chapter 2 is under review in *PNAS*, and Chapters 3-5 are in preparation for submission. I draw together the key findings of Chapter 2-5 in Chapter 6, highlighting general conclusions and future research directions.

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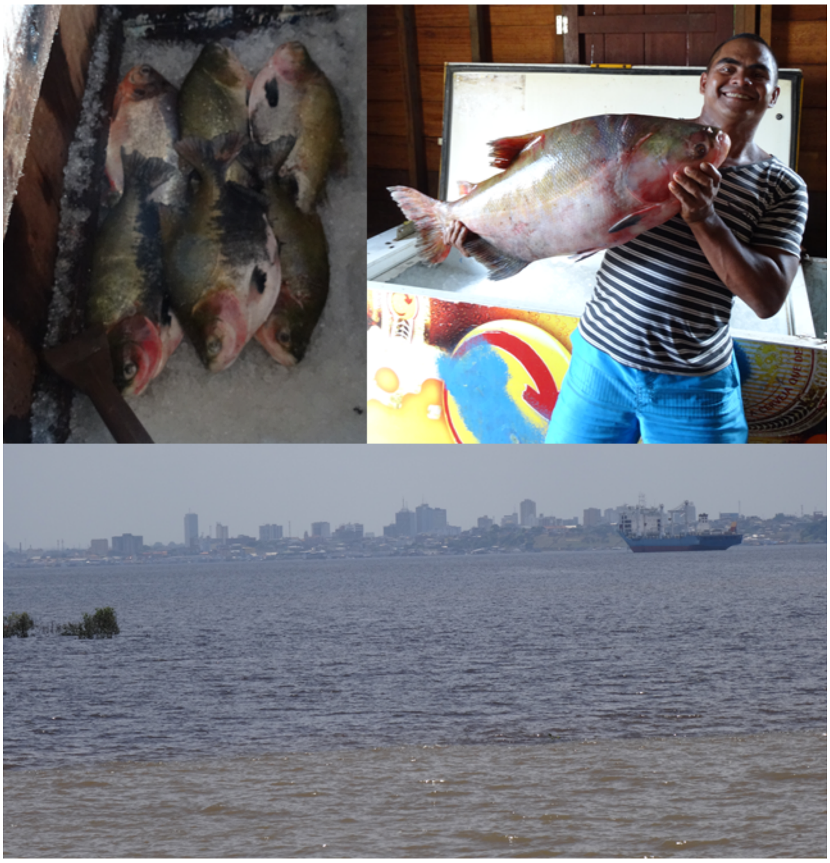
Chapter 2

RAINFOREST METROPOLIS CASTS 1000 KM DEFAUNATION SHADOW



Top-left: tambaqui (*Colossoma macropomum*) fish on ice and destined for Manaus, top-right: a 13 kg tambaqui - a large and valuable catch these days, bottom: looking back at Manaus on the way to the River Purus. Photo credits: Daniel Tregidgo

Rainforest metropolis casts 1000 km defaunation shadow

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2.1. Abstract

Tropical rainforest regions are urbanising rapidly, yet the role of emerging metropolises in driving wildlife overharvesting in forests and inland waters is unknown. We present the first evidence of a large defaunation shadow around a rainforest metropolis. Using interviews with 392 rural fishers we show that fishing has severely depleted a large-bodied keystone fish species, tambaqui (*Colossoma macropomum*), with an impact extending over 1000 km from the rainforest city of Manaus (population 2.1 million). There were strong signals of defaunation within this area, including a 50% reduction in body size and catch rate (catch-per-unit-effort). Our findings link these declines to city-based boats that provide rural fishers with reliable access to fish-buyers and ice, and likely impact rural fisher livelihoods and flooded forest biodiversity. This novel empirical evidence that urban markets can defaunate deep into rainforest wilderness has implications for other urbanising socio-ecological systems.

Key words: ecological footprint, freshwater biodiversity, fishing down, overfishing, urbanisation

2.2. Introduction

The tropics harbour two-thirds of the Earth's biodiversity (Dirzo & Raven 2003), and are experiencing rapid human population increase, urbanisation and economic transitions (Fig. S2.1). These demographic changes are resulting in higher food demand from tropical consumers, particularly for animal protein (Sans & Combris 2015). Much of this demand is being met by the expansion of farmed meat production, which has resulted in widespread land-use change (Foley *et al.* 2005). However, wild meat such as fish and bushmeat is also an important food for hundreds of millions of tropical consumers, from the poorest and most vulnerable people (Milner-Gulland & Bennett 2003; Béné *et al.* 2015) to wealthier urban residents (Parry, Barlow & Pereira 2014; Shairp *et al.* 2016). The consumption of wild meat is causing pan-tropical defaunation because exploited populations are widely harvested above the maximum sustainable yield (Milner-Gulland & Bennett 2003; Allan *et al.* 2005; Dirzo *et al.* 2014; McCauley *et al.* 2015). The severe decline in abundance of exploited species can cascade onto ecosystem functioning and human well-being, causing food insecurity by reducing access to safe and affordable sources of protein and micronutrients (Dirzo *et al.* 2014; McCauley *et al.* 2015).

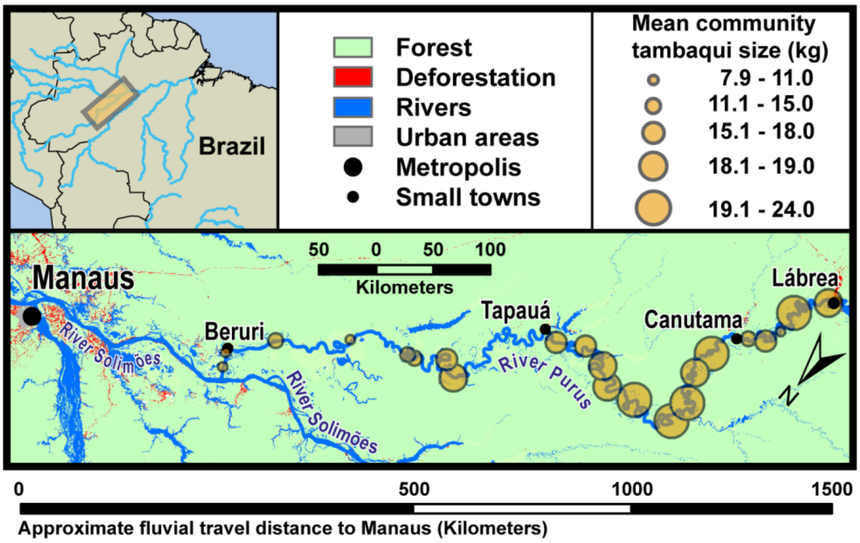

Fig. 2.1. Map of the Purus River. Mean community tambaqui size corresponds to the largest tambaqui caught in the fishers' lives, as presented in Fig. 2.2*A*.

There is now evidence that urban demand is an important driver of tropical wildlife depletion. Marine defaunation shadows have been observed around urban markets, in the form of market proximity-dependent declines in target seafood species, or even whole fish communities (Scales *et al.* 2006; Brewer *et al.* 2009; Maire *et al.* 2016; Cinner *et al.* 2016). Tropical inland fisheries have also been over-exploited (Allan *et al.* 2005), yet evidence is based on local effects of rural-subsistence fishing (Allan *et al.* 2005; Castello, Mcgrath & Beck

2011), so the impacts of overfishing inland waters to supply urban markets are unclear. Modelled bushmeat market data suggesting that rainforest defaunation shadows exist around urban areas (Wilkie & Carpenter 1999; Fa *et al.* 2010; Allebone-Webb *et al.* 2011) are supported by recent empirical evidence that *in situ* terrestrial wildlife population impacts are greatest nearer small towns (Parry & Peres 2015). Although forest degradation has been observed spreading from a tropical forest metropolis to meet demand for wood (Ahrends *et al.* 2010), the role of emerging metropolises (>1 million people) in driving large-scale wildlife overharvesting in rainforests and/or inland waters is unknown.

Understanding metropolitan impacts on biodiversity and ecosystems is critical in the Amazon, the world's largest tropical rainforest and drainage basin with over 1 million km^2 of freshwater ecosystems (Castello *et al.* 2013) and more fish species than the Congo and Mekong basins combined (Winemiller *et al.* 2016). Human demographic changes in the Amazon illustrate how the demand for wild meat harvest has urbanised. Three quarters of the population of the Brazilian Amazon lived in rural areas in 1950, whereas three quarters - around 18 million people - now live in urban areas (IBGE 2010a). Recent evidence shows that urban consumption of wild meat in Amazonia is commonplace (Parry, Barlow & Pereira 2014), as is the case across the forested tropics (Milner-Gulland & Bennett 2003) where urbanisation continues (Fig. S2.2). This raises an important question about the defaunation shadows cast by rainforest cities, in particular large metropolises, in so-called tropical 'wilderness' areas of largely structurally intact rainforest and sparse human population (Mittermeier *et al.* 1998).

For the first time, we examine how far the defaunation shadow of a metropolis extends into the forested 'wilderness'. We then assess which factors determine the extent of this shadow, and estimate the potential ecological and social consequences. Specifically, we use fisher surveys to investigate the impacts of feeding the Amazon's largest city, Manaus, by harvesting its consumer's favourite fish species, tambaqui (*Colossoma macropomum*). Through these surveys we measure the principal indicators of overharvesting for targeted fish species; the captured individual's body size and catch-per-unit-effort in biomass (CPUEb) (Allan *et al.* 2005). We surveyed a 1267 km fluvial travel distance gradient along the Purus River, which is Manaus' principal fishing ground.

The Purus watershed has very low human population densities and high remaining forest cover (Fig. 2.1; Table S2.1), bringing our study area well within the definition of a tropical wilderness area (Mittermeier *et al.* 1998). It is also one of just three major Amazonian tributaries with an undammed main channel, and the only one whose watershed remains wholly undammed (Winemiller *et al.* 2016). By collecting these data in a heavily fished but otherwise relatively pristine area, we hypothesise that there will be a measurable decline in the indicators or tambaqui overharvesting with increasing proximity to the city of Manaus.

2.3. Results

2.3.1. Spatial decline in tambaqui

Fishers nearer Manaus reported catching tambaqui half the size of those caught 1000 km from the city (Fig. 2.2A and B). The size of the largest tambaqui caught in the fisher's lifetime increased significantly with distance from Manaus (n = 392, P < 0.001), as did the mean size caught in the 72 hours prior to the interview (n = 51, P = 0.003). The tambaqui catch rate also doubled with increasing distance along the Manaus travel-distance gradient (Fig. 2.2*D*), with which a positive trend in CPUEb was found (n = 46, P = 0.035). Reductions in the gill net mesh size used to catch tambaqui were also found with increasing proximity to the city (n = 46, P = 0.002; Fig. 2.2*C*), indicating that fishers here do not expect to catch larger individuals. Flooded forest cover was included as a model variable as it represents essential tambaqui feeding habitat, but showed no significant trends. Apart from distance to Manaus, the only significant variables in any of the four models showed a positive relationship between distance to the nearest town and the size of the largest tambaqui caught in in the fisher's lifetime (P = 0.022; Table S2.1), and a negative relationship between gillnet mesh size and human population density (P = 0.021). The slight dip in all four tambaqui population indices at greater distances from Manaus (Fig. 2.2) is likely explained by the presence of a road just upstream of our study area that connects this upper section of the River Purus to other distant urban markets.

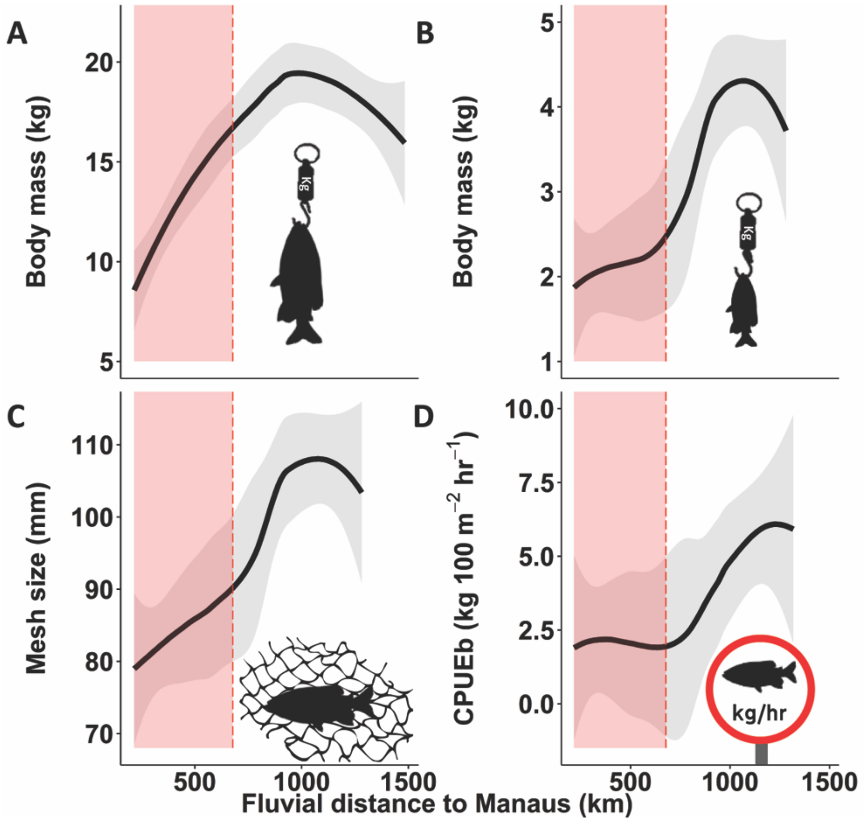

Fig. 2.2. Spatial declines in tambaqui (*Colossoma macropomum*) towards Manaus. Relationships between fluvial travel distance to Manaus and (**A**) the largest tambaqui caught in the fisher's lifetime (kg), (**B**) the mean sized tambaqui caught recently (kg), (**C**) the gill-net mesh size (mm) used to catch a tambaqui, and (**D**) tambaqui CPUEb (catch-per-unit-effort in biomass; kg per 100 m^2 of gill net and one hour of fishing). B to D represent fishing activity within 72 hours prior to interview. Red shaded areas depict the range in which fishers have regular access to fish-buyers and ice. Shown in grey are 95% confidence intervals.

2.3.2. Mechanism

We identify boats from Manaus buying fish as the principal mechanism explaining tambaqui decline. Field observations and our analytical results demonstrate that the fluvial gradient we surveyed can be split into two sub-systems. Commercial fishing is facilitated in rural communities closer to Manaus by boats that deposit ice and buy fish from local fishers at least once a week (shaded red in Figures 2*A* to *D*). Upstream of this, fishers sell fish independently when possible. Modelled trends of tambaqui capture from recent fishing activity (Figs. 2*B* to 2*D*) show clear inflection points, with steepening inclines in tambaqui demographic indicators upstream of regular fish-buyer routes. Communities receiving frequent visits from fish-buying boats reported the smallest tambaqui (largest in lifetime; *P* <

0.001, and mean in the 72 hours prior to interview; $P < 0.001$), the smallest mesh sizes used to catch them ($P < 0.001$), and the lowest CPUEb ($P = 0.02$; Fig. S2.3).

2.3.3. Ecosystem function

To examine the potential ecological consequences of tambaqui defaunation on the Amazon's flooded forest, we simulated the impacts of over-harvesting tambaqui for seed dispersal by combining our mean body size data model (Fig. 2.2*B*) with a published model of median seed dispersal distance (Anderson *et al.* 2011). Our simulations predict that tambaqui 1350 km upriver from Manaus will disperse seeds twice as far (337 m) as those 300 km from Manaus (168 m; Fig. S2.4).

2.4. Discussion

This decline in tambaqui size (Fig. 2.2) represents a gradient of impacts, which extends over 1000 km from the metropolitan market center of Manaus. Economically, the loss of large tambaqui is important, as larger individuals are the most valuable per kilogram, with larger fish (≥7kg) worth 3.4 times per kilogram more to the fisher than the mean fish reportedly caught in this study (2.9kg) (Table S2.2). This is critically important in our study region because the primary source of rural earnings is selling fish (Fig. S2.5). Hence, large-scale spatial declines is evidence that the unsustainable trade in tambaqui to Manaus threatens long-term livelihood security hundreds of kilometres away, and may increase existing high reliance on conditional cash transfers as a main income source for many households (Fig. S2.5).

The spatially-dependent size-profile of tambaqui harvests is a key indicator of population status, and provides strong evidence that fishing pressure driven by demand from Manaus has caused the depletion of tambaqui. Both within and across species, large-bodied animals tend to be the most impacted by wildlife consumption, because they are intrinsically vulnerable to over-harvesting (Milner-Gulland & Bennett 2003; Allan *et al.* 2005) and preferred by harvesters (higher returns on effort) and consumers (Allan *et al.* 2005), many of whom covet rarity (Shairp *et al.* 2016). Urban consumers can therefore maintain strong demand for a small number of increasingly rare species (Shairp *et al.* 2016), and are willing to pay high prices for large individuals.

The loss of large freshwater fish species or size classes can trigger ecological cascades because they are often top apex predators with central roles in food web dynamics (Allan *et* *al.* 2005), or perform disproportionately important ecological functions, such as carbon flow modulation (Taylor, Flecker & Hall Jr 2006) and seed dispersal (Correa *et al.* 2015). Tambaqui can disperse seeds farther than almost any frugivorous animal yet studied, and this dispersal distance increases with body size (Anderson *et al.* 2011). The major reductions in long-distance seed dispersal modelled in this study could inhibit the ability of tambaqui-dispersed seed species to germinate successfully, colonize unoccupied and distant patches and maintain gene flow across fragmented plant populations (Anderson, Rojas & Flecker 2009; Anderson *et al.* 2011; Correa *et al.* 2015).

The strong spatial decline in the size of the largest tambaqui caught in the lifetime of fishers (Fig. 2.2*A*) indicates that Manaus has driven a spatially expanding depletion shadow of tambaqui over the past decades. This sequential exploitation may well have started with the over-harvesting of fisheries near Manaus, followed by fish-buyers travelling further afield to find more intact tambaqui populations. This interpretation is supported by findings in the 1980s that CPUEn (catch-per-unit-effort in numbers) of tambaqui was lower in lakes nearer Manaus (Petrere Jr. 1986). Since then, however, Manaus has thrived economically and its population has doubled (Fig. S2.6). According to official statistics, the resultant growing demand for tambaqui is mainly being met by a rapidly expanding aquaculture industry, while the reported wild catch has fallen. However, study of the Manaus market shows that the wild tambaqui landing data are vastly underestimated, due to widespread concealed landings of small wild tambaqui (Araujo-Lima & Goulding 1997; Santos, Ferreira & Zuanon 2006) below the legal threshold (<55cm ≈ 4.3 kg), which consumers prefer to farmed individuals.

We present the first evidence of a large-scale spatially-dependent defaunation shadow around a rainforest metropolis, using the case of the tambaqui fishery around Manaus, home to more than two million people. Our findings have shown how these impacts are driven by urban demand for a high-value fish species, which also has a key role in the ecology of biodiversity-rich flooded forest. This study advances recent findings that anthropogenic impacts in terrestrial and marine systems are strongly determined by distance from cities (Ahrends *et al.* 2010) or market access (Brewer *et al.* 2009; Maire *et al.* 2016; Cinner *et al.* 2016). Our research therefore also contributes to evidence (Parry, Barlow & Pereira 2014) refuting assertions that urbanisation and resulting rural depopulation in the forested tropics will reduce harvesting impacts on biodiversity (Aide & Grau 2004; Wright & Muller-Landau 2006). Finally, our findings may offer a warning for tropical Asia and Africa.

While urbanisation and the economy of the Amazon rainforest's main host nation (Brazil) currently surpasses that of the Congo (Democratic Republic of Congo) and Southeast Asian (Indonesia) rainforests, these regions are also experiencing rapid economic growth and urbanisation (Fig. S2.2), which is likely to increase the defaunation shadows of rainforest cities there.

2.5. Materials and Methods

2.5.1. Study Area

The study was carried out in rural communities situated along the River Purus in the Brazilian Amazon (Fig. 2.1). The river offers a unique system to study overfishing in an otherwise relatively pristine environment. The River Purus supplies more fish to the Amazon's largest city, Manaus (population 2.1 million people; IBGE, 2010), than any other river (Batista & Petrere Júnior 2003; Cardoso *et al.* 2004; Gandra 2010). However apart from high fishing pressure, it does not suffer significantly from the other major threats of Amazonian freshwater degradation; deforestation, pollution and dam construction (Castello *et al.* 2013). The Purus River catchment meets the definition of a wilderness area (Mittermeier *et al.* 1998), with high remaining forest cover, and low population densities (Table 1.2). It is the only major Amazonian tributary whose watershed remains undammed, and one of three with an undammed main channel (Winemiller *et al.* 2016).

Tambaqui was selected as our focal wildlife species both due to its socioecological importance, and because we believed that it presented us with the best chance of detecting overfishing induced spatial population trends, which are commonly masked in freshwater systems by a synergy of other pressures (Castello *et al.* 2013). Tambaqui is the most commercially valuable wild fish species in the region (Table S2.2), and the most popular fish food species among our rural study population (Fig. S2.7) and Manaus residents (Fig. S2.8). It is also one of few Amazonian fish species thought to have witnessed wild stock declines (Merona & Bittencourt 1988; Isaac & Ruffino 1996; Castello *et al.* 2013); once being the most landed species in Manaus, but seeing dramatic declines in landed catch (Merona & Bittencourt 1988) and body size (Costa-Pereira & Galetti 2015). Lastly, tambaqui has been identified as a high-quality seed disperser in the *várzea* flooded forest, and they disperse seeds longer distances than almost any frugivore (terrestrial or aquatic) reported in the literature (Anderson *et al.* 2011).

2.5.2. Sampling

We worked downstream of the town of Lábrea and upstream from the confluence with the River Solimões. From the first to the last community the fluvial travel distance along the River Purus was 1267 km, as calculated using the travel network function in ArcGIS 10.2.2 (ESRI 2014). We would stop at the first community we came to as we travelled downstream from Lábrea that had 10-35 ordinarily (not necessarily currently) inhabited houses, and we would not stop at another community for a minimum of 13 km (mean 61 km) fluvial travel distance subsequently. Market access was indicated solely as fluvial travel distance to Manaus because the studied section of the River Purus contains no roads, and all transport is via the river network. We did not work in the stretch of the river covered by the Abufari Biological Reserve, as regulation and monitoring concerning harvesting practices were much more intense than in sustainable use reserves or unprotected areas, potentially causing unnecessary variation in results; both ecological, and in terms of response-bias.

We visited a maximum of 20 households per community. Where a community had more than 20 households, those to be visited would be selected randomly in a lottery system. We interviewed every household member of 16 years of age or older that had been fishing in the past 30 days (referred to as a fisher). Guided by average river levels (Coe *et al.* 2002), we visited each community at its approximate high water peak (April – July 2014) to reduce the variation in ecology and fisher activity caused by the flood pulse (Junk, Bayley & Sparks 1989), thereby also avoiding working during the *defeso* fishing closed season.

2.5.3. Interview Questions

All fishers were asked in detail about the catch, effort and catch methods of every fishing trip that they had undertaken in the 72 hours prior to the interview. Where tambaqui was caught, they were asked to recall the number of individuals and estimated weight of the catch. To calculate effort, we asked fishers when they left and returned to their house, how long the return journey took, and how long they spent harvesting if they were not harvesting for the entire period that they were away from home and not travelling. For fishing net dimensions, we asked the mesh size (distance of the mesh between opposite knots in mm), length, and height. The length and height were used to calculate the net area. The largest fishing net mesh size used on a fishing trip that caught a tambaqui was used as a datapoint in the mesh size analysis as we do not know which net specifically caught tambaqui, and because tambaqui would usually be the largest targeted fish.

2.5.4. Use of interviews for collection of ecological data

There is a severe lack of data on harvesting of large and rare animals in rural tropical settings due to logistical difficulties, and due to difficulty in detection of such animals. Because of this, combined with the enormous geographical scale of the study area, this study required a much more efficient data collection method than standard scientific fish sampling. Interviews have been used increasingly in ecological studies to collect the knowledge of rural people, particularly harvesters. Compared to traditional techniques, harvester CPUE (catch-per-unit-effort) has been shown to be much cheaper, more efficient, and result in similar levels of accuracy (Jones *et al.* 2008; Rist *et al.* 2010; Tesfamichael, Pitcher & Pauly 2014). One increasingly popular use of harvester interviews is the collection of catch and effort data, in order to undertake analyses on catch, effort, and CPUE. Commercial CPUE is probably the most widely used index of abundance in fisheries (Edwards *et al.* 2012), and is being increasingly commonly used in studies of freshwater fisheries (Almeida, Lorenzen & Mcgrath 2002; Hallwass *et al.* 2011; Pinho, Orlove & Lubell 2012). Hence, harvester recall data on fished tambaqui body size, CPUE and fishing net mesh size we used to indicate the species' population status.

2.5.5. Statistical Analysis

Statistical analyses were performed in R statistical software version 3.2.3 (R Core Team 2015). Linear mixed models combining primary response variable data with secondary explanatory variable data were used for multivariate analyses. Response variables were quantitative responses to fisher surveys. Response variables were (1) the largest tambaqui individual caught by a fisher in their lifetime (kg), (2) the mean tambaqui caught by a fisher in the 72 hours prior to interview (kg), (3) the maximum gill net mesh size used on a fishing trip that caught tambaqui (mm), and (4) CPUEb in kg per 100 m^2 of net deployed, per hour it was in the water. To keep response variables spatially associated with each community's location, each response variable concerned only fishing trips that had occurred within 2 hours *rabeta* motorised canoe journey from the fisher's home in the community. This is a measure that local people can relate to and that is fairly standard, as most harvesting is undertaken using motorised canoes of similar power (generally 5.5 horse-power) that travel at around 9 km h^{-1} (Parry & Peres 2015). Community was used as a random variable in all models. Model diagnostic plots were subsequently inspected.

Explanatory variables were fluvial distance from Manaus (km), fluvial distance from the closest town (Lábrea, Canutama, Tapauá or Beruri) (km), human population density (people per km^2), and percentage flooded forest (*várzea*) cover within a 5 km radius of the community. Human population density was calculated as the 2010 Brazilian census population of the census sector in which the relevant community was located (IBGE 2010a), divided by the area of that census sector (calculated in ArcMap (ESRI 2014)).

Percentage flooded forest area was included because most tambaqui were caught in the flooded forest, which is an essential tambaqui feeding habitat (Araujo-Lima & Goulding 1997). To calculate this we initially made a flooded forest map of the study area in ArcMap (ESRI 2014), which consisted of the area defined as forest (TerraClass landcover map (Instituto Nacional de Pesquisas Espaciais (INPE) 2010)) that spatially coincided with the area that is permanently or seasonally flooded (floodplain map). A buffer with a 5 km radius was then created around each community, and the percentage of this area covered by flooded forest was calculated. This percentage ranged between 16.3-92.2% (mean 59.0%), but there was no significant trend with distance to Manaus ($P = 0.5$).

2.5.6. Ethics

On arrival to every community we would initially approach the principal community representative (*presidente*) to thoroughly explain the research and ask permission to work in the community. A further explanation of the research was given on arrival at every interviewed household. Oral permission was obtained before proceeding with research, which was seen as more ethically sound than written permission in an area with high illiteracy rates. The research was assessed and approved by ethics committees at both Lancaster University (UK) and the Federal University of Lavras (Brazil). Article 37 of Brazilian law 9605 from 1998 states that killing an animal is not a crime when it is carried out to satisfy the hunger of the harvester or their family. At no point in this paper was it stated whether any of the sampled fish were sold or used for consumption, and therefore no activity presented in this paper can be perceived as illegal.

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2.8. Supplementary Information

2.8.1. Supplementary figures

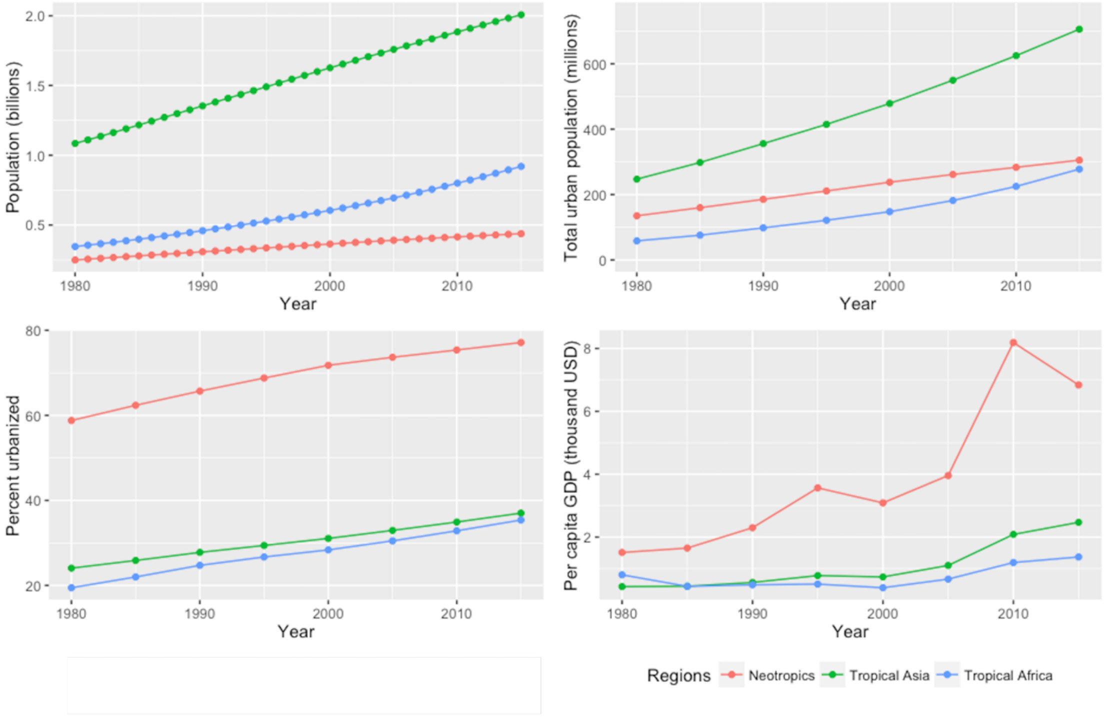

Fig S2.1. Demographic and economic change in the tropics by region (1980-2015). The tropics here are defined as all the countries whose centroids lie within 23.5◦ of the equator (ArcMap (ESRI 2014)). Tropical Asia includes the Pacific island nations of Oceania. Data sources: UN Population Division (UN 2015); IMF World Economic Outlook Database (International Monetary Fund 2016). GDP is based on current prices.

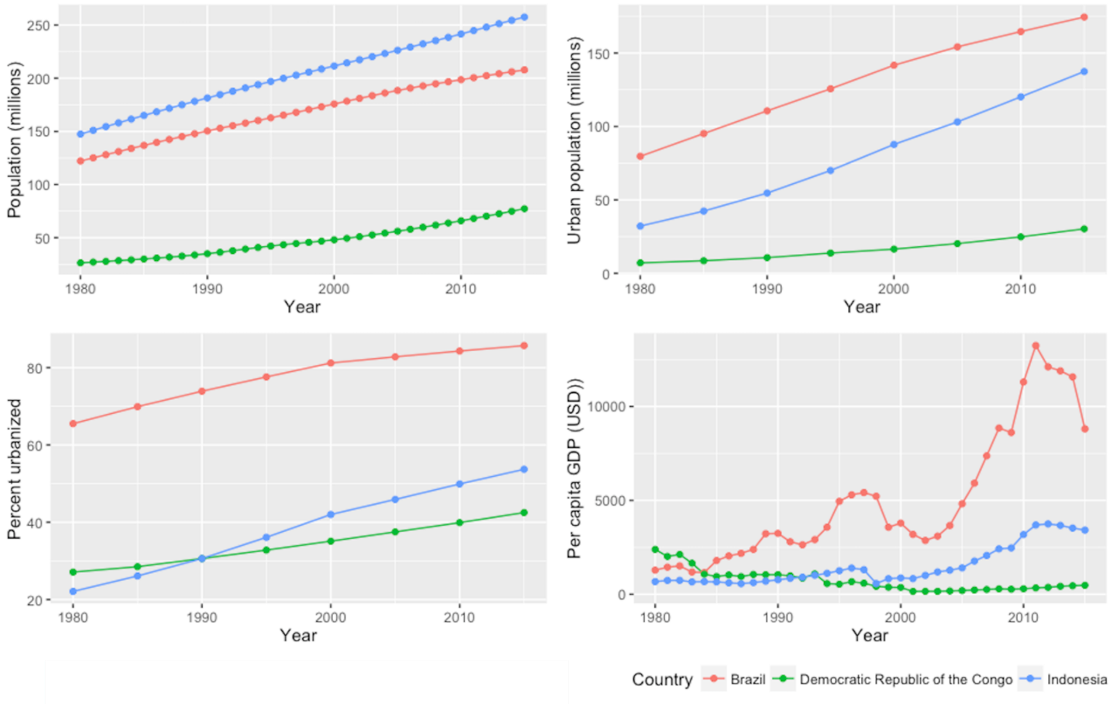

Fig S2.2. Demographic and economic change in the major national hosts of tropical forests (1980-2015). The countries with the largest areas of tropical forest are (in descending order) Brazil, the Democratic Republic of Congo and Indonesia (Saatchi *et al.* 2011).

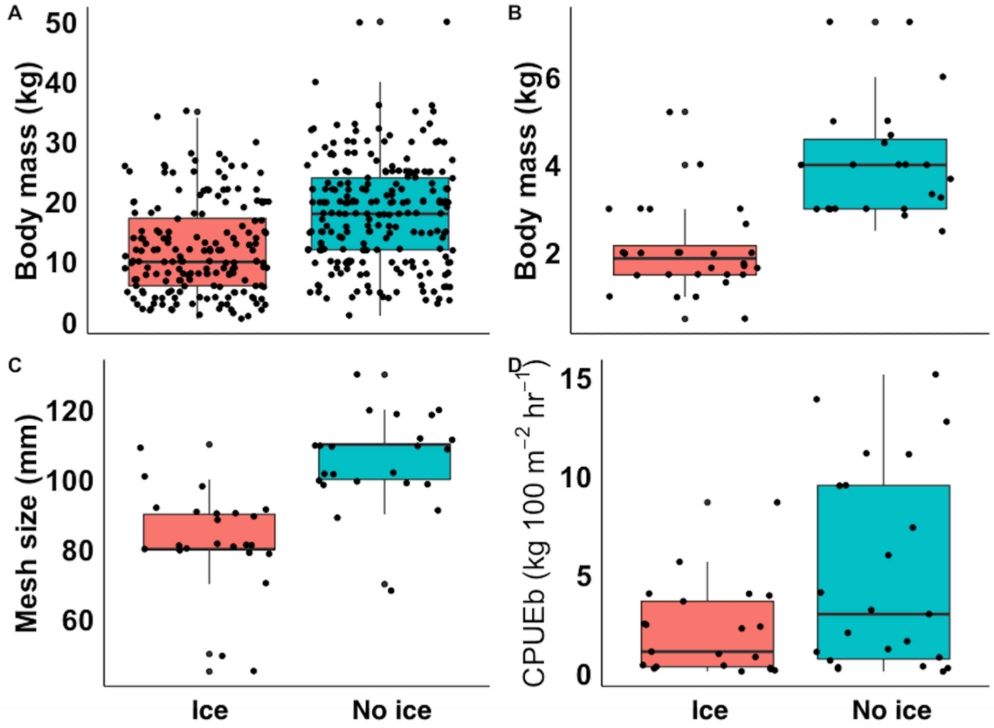

Fig. S2.3. The proposed mechanism for tambaqui decline is access to city-based boats that supply ice and buy fish. Comparing communities that receive regular city-based boat visits (red) and those that do not (blue) in terms of (**A**) the largest tambaqui caught in the fisher's lifetime (kg), (**B**) the mean tambaqui caught in the 72 hours prior to interview (kg), (**C**) the mesh size used to catch a tambaqui (mm), and (**D**) tambaqui CPUEb (kg 100m^2 hour^{-1}).

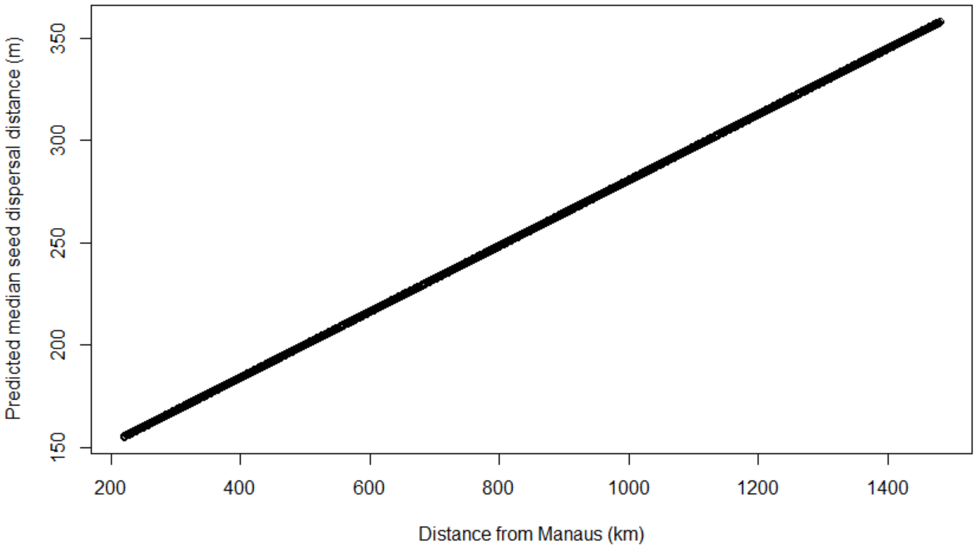

Fig. S2.4. Predicted median seed dispersal distance as a function of distance from Manaus. Model predictions made from primary data on mean tambaqui sizes caught in the 72 hours prior to interview (Fig. 2.2B), and secondary seed dispersal distance data (Anderson *et al.* 2011).

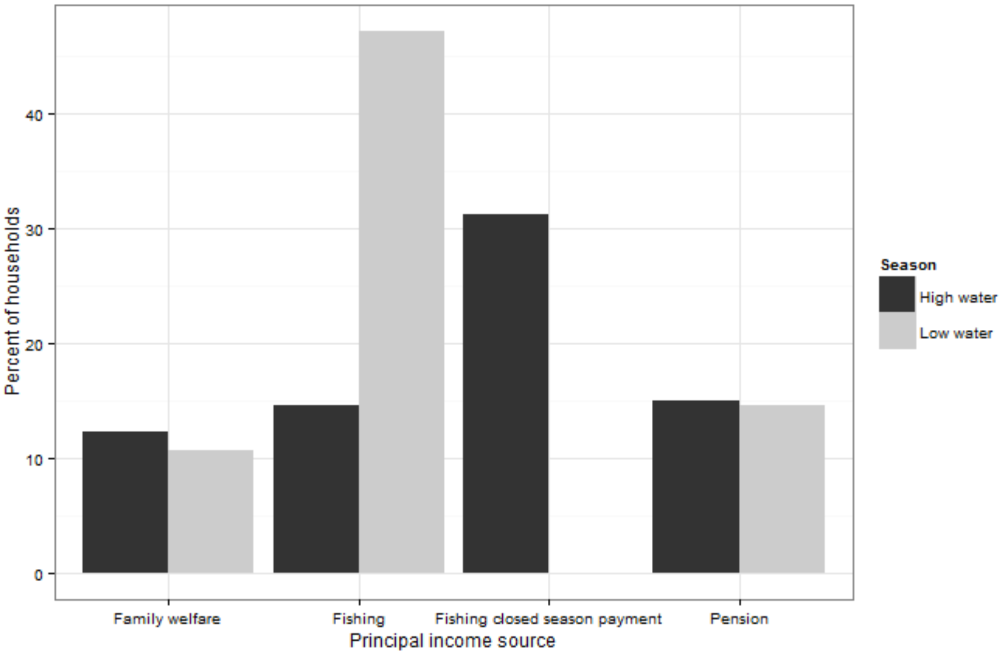

Fig. S2.5. Main source of income for interviewed households by season. Shown here are the principal income sources, which collectively constitute over 70% of households in either high or low water seasons: family welfare (*Bolsa familia*), fishing (*pesca*), fishing closed season payments (*defeso*), and pension (*aposentadoria*) pension.

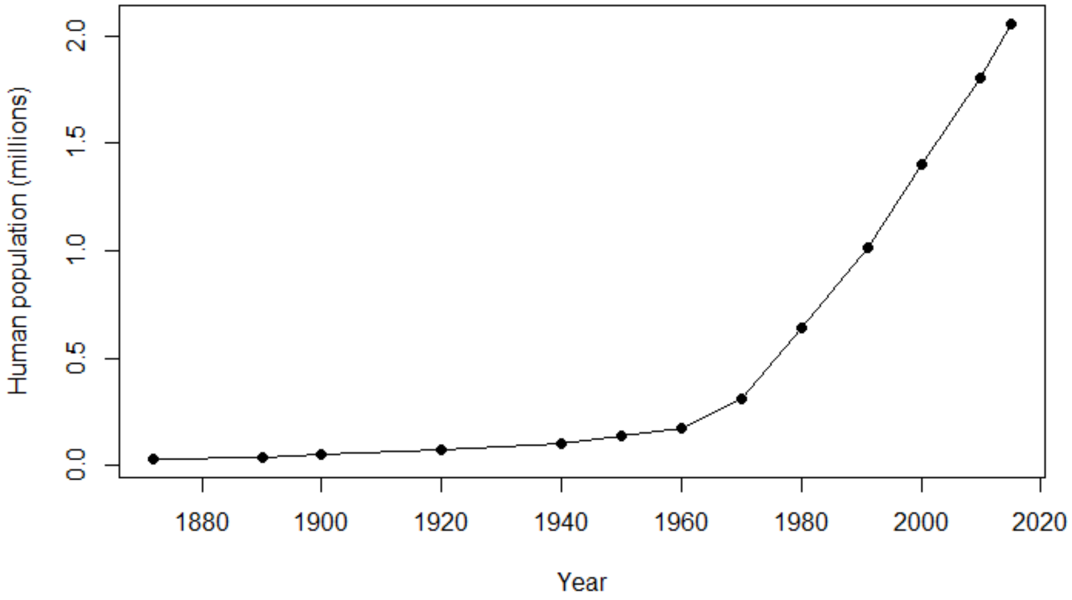

Fig S2.6. Human population of Manaus. Data from 1872-2010 census, and 2015 data point (y = 2,057,711) is an official IBGE estimate (IBGE 2010a).

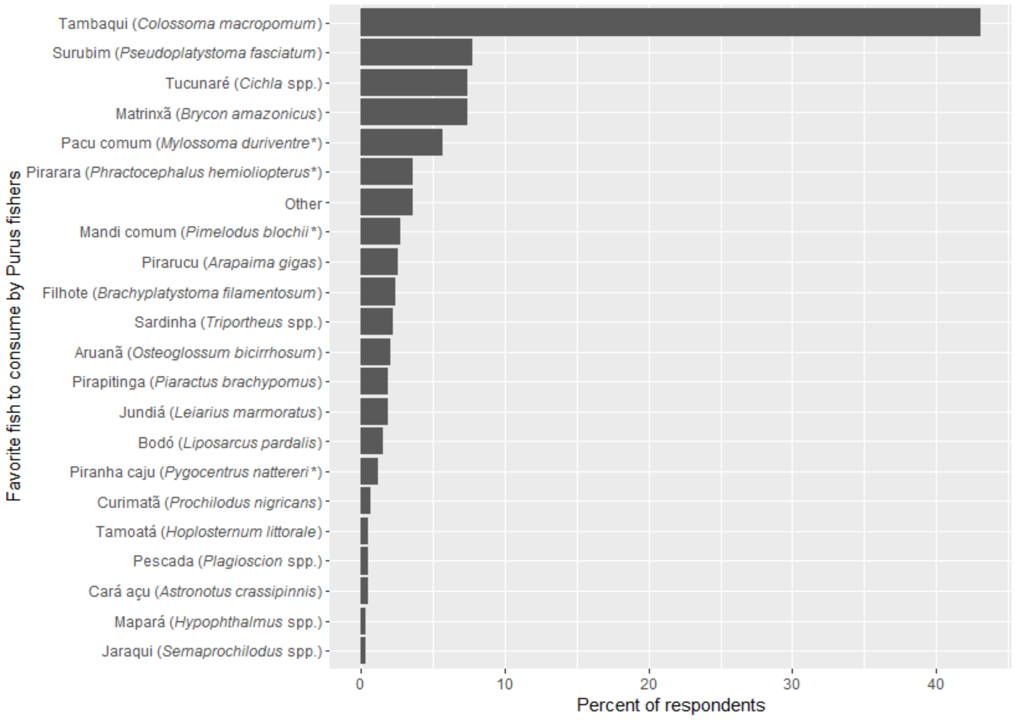

Fig. S2.7. Favourite fish taxa consumed by Purus fishers. All sampled household residents aged 16 or over that had fished in the past 30 days (n = 582) were asked “what is your favourite fish to eat?”

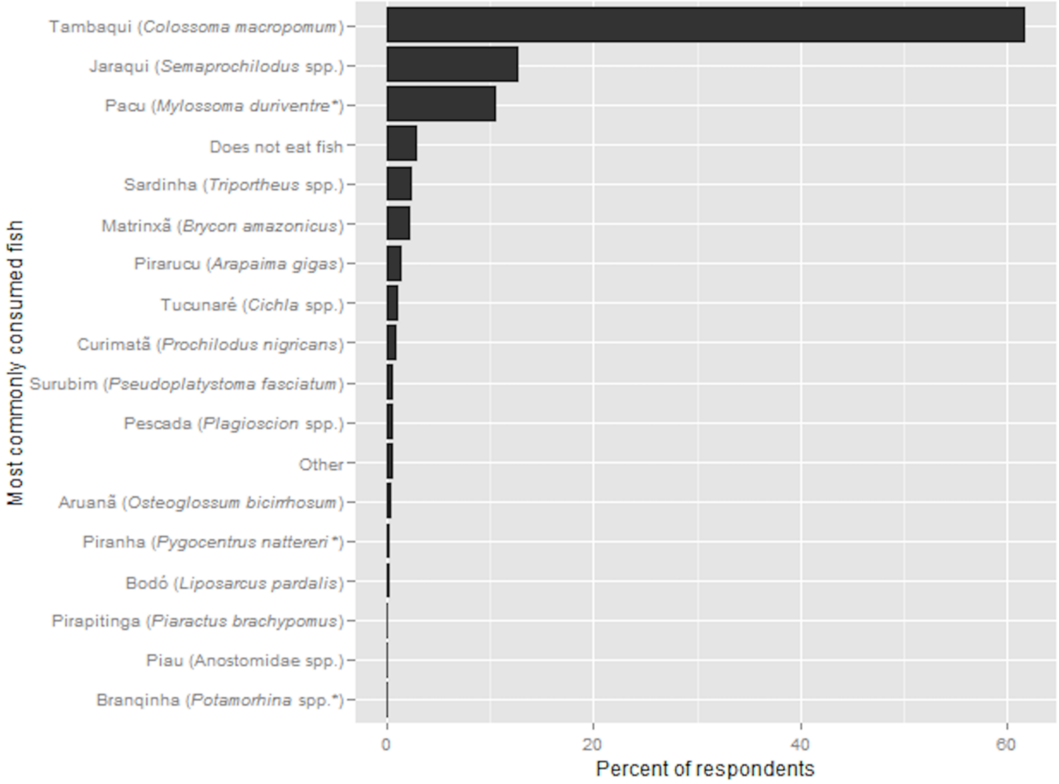

Fig. S2.8. Most commonly consumed fish taxa in Manaus. Data from a market survey where 1000 Manaus residents sampled across socio-economic groups were asked "what type of fish do you eat most?" (Pesquisa365 2015). *The local names *pacu*, *piranha* and *branquinha* are used to describe various genera, however the Manaus markets are dominated by the species or genera written in parentheses (Santos, Ferreira & Zuanon 2006).

2.8.2. Supplementary tables

Table S2.1. Linear mixed model results

	Biggest in lifetime				Mean in 72 hours				Mesh size				CPUEb			
n	392				51				46				46			
	Estimate	SE	t	*P*	Estimate	SE	t	*P*	Estimate	SE	t	*P*	Estimate	SE	t	*P*
Distance to Manaus	**0.007**	**0.001**	**5.1**	**<0.001**	**0.003**	**0.001**	**4.4**	**0.002**	**0.024**	**0.007**	3.6	**0.002**	<0.001	<0.001	**2.6**	**0.035**
Distance to nearest town	**0.017**	**0.007**	**2.4**	**0.022**	0.001	0.002	0.7	0.488	0.043	0.024	1.8	0.077	<0.001	<0.001	-0.9	0.355
Population density	-1.329	0.813	-1.64	0.123	-0.148	0.399	-0.4	0.711	**-13.637**	**5.726**	**-2.4**	**0.021**	0.016	0.017	0.9	0.347
Percentage flooded forest cover	0.018	0.027	0.7	0.526	-0.005	0.011	-0.4	0.669	-0.193	0.123	-1.6	0.122	<0.001	<0.001	1.3	0.187

Table S2.2. Tambaqui price in Brazilian Reals (BRL) paid to fishers by size class, as defined by local fish buyers in the lower Purus

Body mass (kg)	Price per kg (BRL)
≥ 7	12
≥ 4 & <7	8
≥ 3 & < 4	5
≥ 2 & < 3	3.5
≥ 1 & < 2	2
< 1	1

Chapter 3

TOUGH FISHING IN THE FLOODED-FOREST: SEVERE SEASONAL FOOD INSECURITY IN A WELL-CONSERVED REGION OF AMAZONIA

Left: going home empty handed is relatively common during high waters, photo credit: Daniel Tregidgo, top-right: a good haul of jaraqui (*Semaprochilodus* spp.) during the low water season, photo credit: Mayana de Almeida Rocha, bottom-right: undertaking a focus group with local people to determine which food insecurity coping strategies were considered most severe, photo credit: Mayana de Almeida Rocha.

Tough fishing in the flooded-forest: Severe seasonal food insecurity in a well-conserved region of Amazonia

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3.1. Abstract

Over a quarter of the world's population suffer from malnutrition, which can result from temporarily reduced access to safe and affordable nutritious food (transitory food insecurity) during shocks or lean seasons. Societies dependent on fisheries encounter seasonal dips in catch rates (catch-per-unit-effort) of exploited species and communities. Yet, research to-date has largely neglected the potential linkages between wildlife catch rates and seasonal food security. The Amazonian flooded forest is relatively intact and is abundant in wildlife, although availability of food resources is highly seasonal and impacted by overfishing. In this paper we investigate whether fish catch rate is linked to food insecurity, and explore its household determinants during the lean season. We collected fishing, hunting and food insecurity interview data during rural household visits (n = 556) over a spatial gradient (1267 km) of commercial fishing pressure in both the high water and low water seasons. In this first study to simultaneously present empirical data on both wildlife catch rates and food security, we show that both suffered significantly during the high water season, with the fish catch rate 370 % greater in the low water season. However, despite overfishing closer to the metropolitan centre of Manaus, we found that neither fish catch rate nor food insecurity varied along the spatial gradient. Importantly, less-deprived households suffered less from food insecurity during the lean season. Despite the abundance of wildlife in the Amazonian flooded forest, we conclude that rural Amazonians suffer from severe food insecurity in the high water season. Our evidence suggests this is due to reduced fish catch rate, which leads to an increase in fishing and hunting effort. Contrary to previous assumptions, we found that local resource-users maintain catch rates in overfished areas, and that food security is unaffected, or even improved as a result of urban accessibility.

Key words: CPUE, fishing, food security, hunting, nutrition transition, yield

3.2. Introduction

Globally, one in nine people are undernourished (FAO, IFAD & WFP 2015), one in eight are obese (WHO 2015), and over a quarter are micronutrient (mineral and vitamin) deficient (Darnton-Hill *et al.* 2005; Strang 2009; IFPRI 2016). Collectively referred to as malnutrition, these health problems are caused by a combination of non-food factors such as poor sanitary conditions, water quality, and primary health care access, and a high prevalence of infectious diseases (Pinstrup-Andersen 2009), in addition to food insecurity, which affects about 2 billion people worldwide (Wheeler & von Braun 2013). Food security is defined as "a situation that exists when all people, at all times have physical, social and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life" (FAO, IFAD & WFP 2015). As such it includes people that suffer from transitory (as opposed to chronic) food insecurity, in which good access to nutritious food is the norm, restricted only during times of scarcity, such as natural disasters or lean seasons. Transitory food insecurity can have serious and often fatal health implications, particularly when suffered at critical life development stages, with pregnant women (Gernand *et al.* 2016) and children under 5 years (Bailey, West & Black 2015) at greatest risk.

Lean seasons exist in many agricultural, pastoral and foraging societies, and are normally linked with climatic rainfall and temperature cycles. Virtually all farming systems in the developing world have a characteristic seasonal variability in both production and consumption (Ferro-luzzi *et al.* 2001). The agricultural lean season is generally associated with the growing season, and often occurs before rains for pastoralists, and before harvest for agriculturalists (Sullivan 2012), when the previous year's product has been exhausted. During a lean season, defined by reduced availability of a primary food source, those with physical, social and economic access to sufficient, safe and nutritious alternative food may cope by switching (commonly by purchase) in order to maintain a healthy diet. However, those without such access to alternatives may not cope, and therefore suffer from some level of food insecurity, potentially leading to malnutrition.

Even mild food insecurity can be detrimental to children's health (Schmeer & Piperata 2016), and various studies have observed a seasonal loss in bodyweight (wasting) or growth stunting in children (Trowbridge & Stetler 1982; Hoorweg, Foeken & Klaver 1995; Panter-Brick 1997; Ferro-luzzi *et al.* 2001; Hillbruner & Egan 2008). Stunting in children can increase susceptibility to disease and cause irreparable damage to cognitive and physical function (Ferro-luzzi *et al.* 2001). Wasting can make adults more prone to illness, and can be particularly harmful when people lack significant fat stores, as weight is lost from lean tissues such as muscles and internal organs (Ferro-luzzi *et al.* 2001). Additionally, the prevalence of parasitic diseases such as malaria, diarrhoea, typhoid and cholera is often seasonal, and in several tropical systems have been shown to occur more during wet seasons (Devereux, Sabates-Wheeler & Longhurst 2013). Although it is clear that seasonality can have serious food security and health implications for vulnerable groups, seasonal food insecurity is poorly understood (Ferro-luzzi *et al.* 2001; Sullivan 2012), and continues to be neglected in research (Chambers 2012) even though most food insecurity is seasonal, and not due to shocks such as conflicts and natural disasters (Vaitla, Devereux & Swan 2009; Barrett 2010).

The limited literature on seasonal variability in food insecurity focuses on agricultural lean seasons (Abdullah & Wheeler 1985; Chikhungu & Madise 2014), and seasonal food insecurity in wild harvesting systems remains extremely understudied. Wild food harvesting is an essential livelihood activity for many people worldwide, including some of the poorest and most vulnerable (Robinson & Bennett 2002; Béné & Friend 2011; Golden 2016). Wild meats in the form of fish and bushmeat provide the main form of protein for hundreds of millions of people (Milner-Gulland & Bennett 2003; Allan *et al.* 2005; FAO 2012b), as well as being an essential source of fats, calories, and other micronutrients such as iron and zinc (Sirén & Machoa 2008; Sarti *et al.* 2015). For many others, wild meats are not an everyday food source, but they can act as an important safety net during times of scarcity, including in agricultural lean seasons (de Merode, Homewood & Cowlishaw 2004) or extreme events (Takasaki, Barham & Coomes 2010; Coomes *et al.* 2010).

The availability of wild species and communities that are harvested for their meat varies seasonally. For example, more frequent meat consumption has been observed during seasonal influxes of migratory herbivores to a tropical rainforest (Nyahongo *et al.* 2009), while the frequency of fish consumption is greater during the low water season in the seasonally flooded Amazon (Begossi *et al.* 1999; Saint-Paul, Zuanon & Correa 2000; Da Silva & Begossi 2009) and Congo (Poulsen *et al.* 2009) basins. Other cyclical natural events can temporarily reduce wildlife populations available to harvesters, such as the inhibition of the nutrient-rich upwelling on the Peruvian coast which cripples the anchovy fishing industry during El Niño events (Ñiquen & Bouchon 2004).

Aside from natural cyclical variation in resource availability, anthropogenic impacts act as threat multipliers to further reduce availability of resources. For example climate change is increasing the frequency and intensity of droughts, thereby decimating crops, and increasing forest fires, which devastates bushmeat populations (Barlow & Peres 2006; Schmidhuber & Tubiello 2007). Damming rivers has changed water quality, altered hydrological regimes, and inhibited the passage of migratory fish, thereby reducing their populations (Carolsfeld *et al.* 2003; Winemiller *et al.* 2016). Defaunation has reduced populations and body sizes, often as a result of direct harvesting (Dirzo *et al.* 2014; McCauley *et al.* 2015). The natural temporal vulnerability of those dependent on agriculture and wild resources is therefore further intensifying in the light of anthropogenic change (Schmidhuber & Tubiello 2007).

3.2.1. Amazonia

Food insecurity and malnutrition are common among rural Amazonians, with high rates of child malnutrition, iron anaemia and vitamin A deficiency detected among the population (Alencar *et al.* 2007, 2008; Piperata 2007; Piperata *et al.* 2013). Despite the abundance of animal protein within their local environment (Beckerman 1979; Alencar *et al.* 2007) and impressive wildlife harvesting skills, rural Amazonians are inherently vulnerable to food insecurity. This is due to a combination of the socio-economic characteristics of the population (e.g. high levels of illiteracy and poverty (IBGE 2010a)), their remoteness (Maru *et al.* 2014), and their continuing reliance on wild protein and farmed calories (Murrieta & Dufour 2004; van Vliet *et al.* 2015a; Endo, Peres & Haugaasen 2016; Dufour *et al.* 2016), the availability of which is susceptible to significant environmental and market fluctuations. Rural Amazonians are further vulnerable to malnutrition as a result of several non-food factors such as poor sanitation (Piperata 2007), prevalence of parasitic insect-borne, water-borne and intestinal diseases, and poor access to healthcare.

Much of Amazonia's rural population live in or around the *várzea* floodplain (Junk *et al.* 2012), and are known as *ribeirinhos*. The *várzea* has been described as a 'counterfeit paradise' because, on the one hand there is an apparent wealth of animal protein and fertile soils (compared to the upland *terra firme*), and on the other hand, there is highly-seasonal productivity and unpredictable flood events (Meggers 1971). Fish is the main source of protein, and the second most important energy source for *ribeirinhos*, after toasted manioc flour, known as *farinha* (Murrieta & Dufour 2004; van Vliet *et al.* 2015a; Endo, Peres & Haugaasen 2016; Dufour *et al.* 2016). Household accessibility to fish and manioc is highly seasonal, due to the annual flood pulse that can inundate a vast area of the floodplain for up to 6 months per year, raising river levels by as much as 15m (Goulding, Barthem & Ferreira 2003). Specifically, flood waters inundate agricultural land (Denevan 1996), and 'dilute' fish concentration and hence reduce catch rates during the high water season (Saint-Paul, Zuanon & Correa 2000; Pinho, Marengo & Smith 2015).

Aquatic and terrestrial wildlife are further impacted by ever-growing urban markets. The demand for wild meat has urbanised in Amazonia, where decades of rapid urbanisation have raised the urban population from one-quarter of the total population in 1950 to three-quarters today (IBGE 2010a). Technological innovations have transformed Amazonian fisheries, permitting them to supply this growing urban demand. The arrival of gillnets, large diesel-powered vessels and affordable ice has allowed fishers to increase their efficiency (CPUE: catch-per-unit-effort), catch and capacity; technologies which have now overtaken traditional gear (cast nets, hooks, tridents, bows and arrows, harpoons etc.), sail-powered vessels, and fish-salting, respectively (Mcgrath 1989; Mcgrath *et al.* 1993; Castello, Isaac & Thapa 2015). There is also recent evidence that overharvesting has caused defaunation of terrestrial and aquatic species that has occurred in response demand from Amazonian towns and cities hundreds of kilometres away (Parry and Peres 2015; Chapter 2).

The extent of commercial hunting in the Amazon is not well known, and recent evidence demonstrates that urban consumption is not negligible (Parry, Barlow & Pereira 2014; van Vliet *et al.* 2015b), as previously thought (Nasi, Taber & Van Vliet 2011). Subsistence hunting, however, is widespread, and may provide a protein source for river-dwellers, second-only to fish (Endo, Peres & Haugaasen 2016). Other forms of wild protein such as meat from caiman (mainly *Melanosuchus niger* and *Caiman crocodilus*), turtle (mainly *Podocnemis expansa* and *Podocnemis unifilis*) and manatee (*Trichechus inunguis*), eggs from wild birds, caimans and turtles, insects (e.g. *Pachymerus nucleorum*), and freshwater shrimp (e.g. *Macrobrachium amazonicum*) also contribute to *ribeirinho* diets and incomes.

Although fish and manioc continue to dominate their diets, contemporary *ribeirinhos* are undergoing a 'nutrition transition' fuelled by increased cash incomes, in which these traditional foods are being increasingly replaced by domestic meats and industrial and processed foods (Sarti *et al.* 2015; van Vliet *et al.* 2015a; de Jesus Silva *et al.* 2016). Extensive Amazonian cattle ranches have facilitated beef's integration into *ribeirinho* diets, although the cheaper price per unit weight means that chicken makes a greater contribution (Nardoto *et al.* 2011; van Vliet *et al.* 2015a; de Jesus Silva *et al.* 2016). Processed meats (e.g. *salsicha, mortadella* and *calabresa* sausages, and canned fish and *conserva* meat) are also widely consumed, facilitated by relatively low prices. The dietary contribution of industrialised, processed and domestic meats decreases over an urban-rural gradient relative to wild meats (van Vliet *et al.* 2015a). Conversely, while urban Amazonians (most of the population) clearly rely heavily on domestic and processed meats (van Vliet *et al.* 2015a), the contribution of these foods to *ribeirinho* diets may have been overstated because most evidence comes from rural settlements proximate to urban centres (Sarti *et al.* 2015; van Vliet *et al.* 2015a).

The nutrition transition may increase the resilience of *ribeirinhos* by reducing their reliance on inherently variable natural wildlife stocks. However these foods tend to have a lower nutritional value than fresh fish and bushmeat (van Vliet *et al.* 2015a), and are thought to be contributing to forms of malnutrition previously not associated with poorer populations, such as obesity (Popkin & Gordon-Larsen 2004), which is now widespread in Amazonia (Alencar *et al.* 2007; Piperata 2007; Silva *et al.* 2016). Another problem with the overreliance on imported foods is the precarious transport network needed to import them from urban markets. There are 68 cities unconnected by road in the Brazilian Amazon, which are populated by 914 thousand people, and an unknown but much larger number of rural settlements without road links (Parry, personal communication). Therefore, many Amazonians are left vulnerable as access to urban food sources is highly dependent on the river network, much of which becomes unnavigable during low waters and particularly during severe droughts. Furthermore, although a reduced reliance on wild meat decreases direct pressures on harvested wildlife populations, domestic meat production also causes environmental impacts (Foley *et al.* 2005; Naylor *et al.* 2005), with considerable pollution coming from industrial chicken production (Gerber, Opio & Steinfeld 2007), and Amazonian deforestation being largely attributed to beef cattle pastures (Greenpeace 2009; Lapola *et al.* 2014).

Non-food factors further exacerbate food insecurity health risks, and the frequent co-occurrence of both malaria (Katsuragawa *et al.* 2010) and iron-deficiency anaemia (Sarti *et al.* 2015) is a major health concern in the Amazonian floodplain. In Africa, anaemia is responsible for about half-of malarial deaths, and although this remains much less common in Latin America (Quintero *et al.* 2011), a recent nutritional analysis of food intake suggested that dietary deficiencies leave Amazonians susceptible to anaemia (Sarti *et al.* 2015). In some remote rainforest populations multiple dietary sources can provide adequate protein, but bio-available iron is only available from animal source foods (Beaton, Calloway & Murphy 1992; Neumann *et al.* 2003). Because fish tends to have lower iron content than terrestrial meat (Tacon & Metian 2013), *ribeirinhos* with high-fish low-terrestrial-meat diets are particularly prone to anaemia. Additionally, poor sanitation in floodplain communities means that diarrhoea is commonplace (Piperata 2007), leading to the dietary loss of nutrients such as iron (Katona & Katona-Apte 2008). Consequently, even subtle seasonal availability constraints to fish may present significant nutritional risks especially for vulnerable members of society such as children, the elderly and those with pre-existing medical conditions. Moreover, reduced fish availability coincides with reduced fruit and vegetable availability, as flooding of agricultural land becomes more frequent and intense.

Existing vulnerabilities of *ribeirinhos* are being further intensified by anthropogenic impacts. These threat multipliers include anything that can reduce the availability of fish, and the primary threats to freshwater ecosystems in Amazonia have been identified as dam construction, deforestation, overfishing and pollution (largely via mining) (Castello *et al.* 2013). Climate change is another key threat multiplier, impacting *ribeirinhos* though changes in rainfall patterns and resultant river levels. In the past few decades the amplitude of the Amazon basin's river discharge has increased, along with the severity of hydroclimatic events, which have also become less predictable (changed in timing) (Gloor *et al.* 2013; Marengo *et al.* 2013). Although the rapid expansion of human infrastructure and economic activities are predicted to have a far greater impact on fish communities in the Amazon than those anticipated by climate change (Oberdorff *et al.* 2015), the consequent increased severity and duration of floods (Marengo *et al.* 2013) that further reduces fish concentrations will therefore also inhibit fishing catch rates. Increased flooding also inundates housing and schools, reduces agricultural land availability and the length of growing seasons (Winklerprins 1992), and increases disease prevalence (Katsuragawa *et al.* 2010). An increase in the severity and frequency of droughts in recent years can result in mass fish kills, increased human predation of aquatic megafauna (such as manatees;

Trichechus inunguis), and cause many river networks to become unnavigable (Marengo *et al.* 2008, 2013), making millions of Amazonians vulnerable to reduced imported food access. As such these climate-induced changes put *ribeirinhos* at the sharp edge of climate change, which may well push them to exceed the coping strategies that they already adopt.

3.2.2. Key knowledge gaps

Although the most common form of food insecurity is that suffered seasonally (Vaitla, Devereux & Swan 2009; Barrett 2010), in societies dependent on harvesting wildlife this issue has been largely ignored by researchers. Many of the world's poor and most vulnerable people rely on wildlife (fish and bushmeat species) for nutrition, and it is known that wildlife availability is often seasonally restricted. Yet no study to our knowledge has ever simultaneously presented empirical data on both wildlife catch rates and food insecurity. This may be due to the disciplinary nature of much of research relating to wild food harvesting, which also fuels commonly unsupported claims by conservation biologists that biological evidence of selective defaunation is indirect evidence of food insecurity (Golden *et al.* 2011; Castello *et al.* 2013; Parry & Peres 2015). We therefore identify the empirical links between wildlife catch rates and food insecurity as a key knowledge gap.

3.2.3. Research aims, questions, and hypotheses

Here, we examine the environmental and social determinants of household food insecurity in the Amazonian floodplain, and explore which coping strategies *ribeirinhos* employ as a response. We do so by exploring spatiotemporal variation in food insecurity, modelling its hypothesised social determinants, investigating its spatiotemporal co-occurrence with variation in fish catch rate, and in harvesting effort and domestic meat consumption. We investigate the following research themes: (1) How variable is the food insecurity of river-dwelling Amazonians in time and space? (2) Which kinds of rural households are most vulnerable to these spatial and seasonal-temporal constraints? (3) Is spatiotemporal variation in fishing catch rates associated with food insecurity? And, finally, (4) what responses do river-dwellers develop to low spatio-temporal fish catch rate?

We hypothesise that food insecurity will be suffered more so in the high water season and closer to urban centres. We also predict significant variation between households, and we therefore hypothesise that wealthier and more educated households that receive conditional cash transfers (CCTs), and with fewer residents, more of whom are of working age, will suffer the least from food insecurity. We expect the food insecurity of local people to occur when and where fish CPUEb is lower, and that they will respond to these shortages by spending longer hunting and fishing, and by consuming domestic meats more frequently (Table 3.1). We aim to address these hypotheses by collecting quantitative data concerning fishing catch rates, household food insecurity, domestic meat consumption rates and some basic household characteristics, collected over a gradient of travel distance to Manaus, during the peaks of the high and low water seasons.

Table 3.1. Hypotheses of spatiotemporal variation in food insecurity, the measure employed in this study to test them, the rationale behind the hypotheses, and supporting references relating to each of the 4 research areas.

Hypothesis	Measure	Rationale	References
(1) The spatial and temporal drivers of food insecurity			
Food insecurity will be greater…			
…in the high water season	High water and low water season repeated sampling	Diluted fish in high water	Non-specific lean season (1-5)
…closer to metropolitan and provincial urban centres	Fluvial travel distance to the state capital (Manaus) and the closest urban settlement	Depleted fish nearer city	None known
(2) Household vulnerability to food insecurity			
Food insecurity will be less severe where…			
…household wealth is greater	Household floor area	Poor have less purchasing power	(6)
…household population is smaller	Household population size	Food is divided between less people	(6, 7, 8)
...education level is greater	Maximum resident’s years of education	Education is a key determinant of production and social mobility	(6, 7, 9)

…a lower proportion of the household is dependent	Proportion of the household that is of dependent age (<16 and >59 years) to those that are not	Dependents consume, but likely to contribute less to money and food acquisition	(7, 8)
…people receive conditional cash transfers	At least one conditional cash transfer received in the household	This income can be spent on food	*Bolsa Familia* (10), pensions (11)
(3) The importance of fish catch rates in driving food insecurity			
Fish catch rates will be lower…			
…during the high water season	CPUEb (catch-per-unit-effort in biomass)	Dilution in greater volumes of water	(12)
…closer to urban centres	CPUEb	Depletion from commercial overfishing	(12, 13)
(4) Responses to low fish catch rates			
Where and/or when fish catch rates is lower…			
… fishing effort will be greater	Household fishing effort (hours), and the chance of going fishing	Compensatory to try to maintain fish catch	(14, 15)
…hunting effort will be greater	The chance of going hunting	Compensatory to try to maintain overall catch	(12, 16)
… domestic meat consumption will be greater	Frequency of household chicken and beef consumption in the past month	Compensatory to try to maintain animal protein	Fish-domestic meat switch (17, 18)

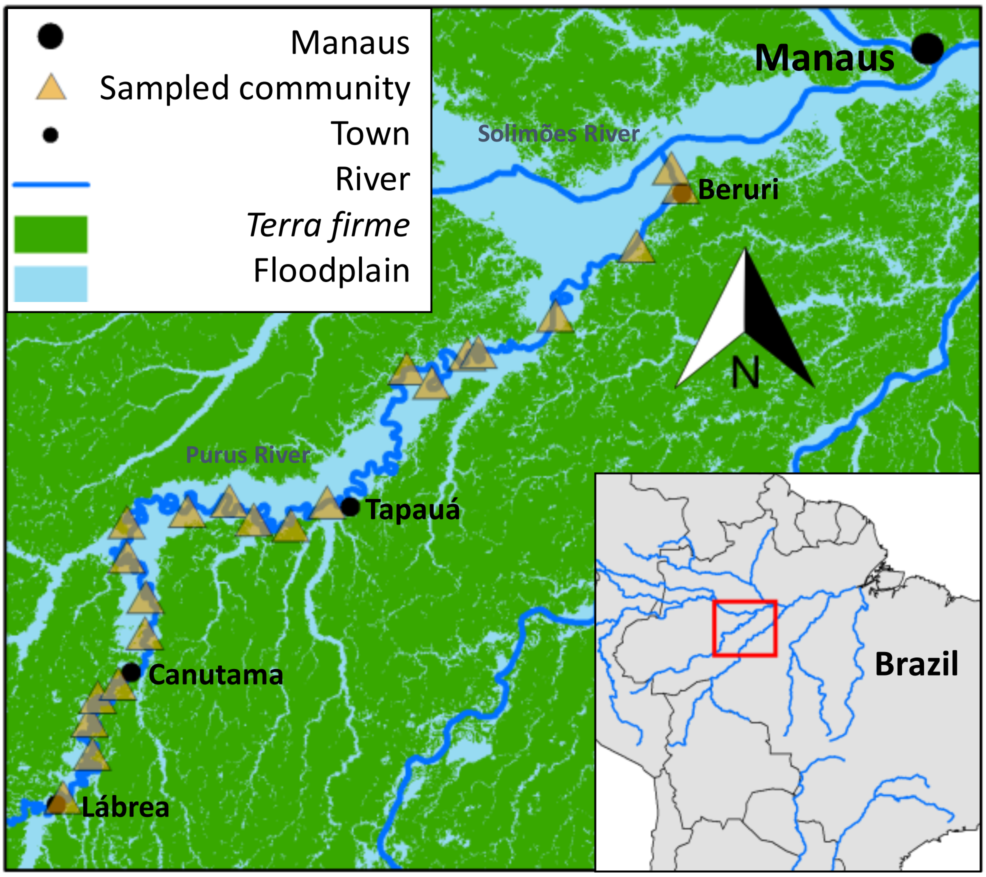
[1-5] (Trowbridge & Stetler 1982; Hoorweg, Foeken & Klaver 1995; Panter-Brick 1997; Ferro-luzzi *et al.* 2001; Hillbruner & Egan 2008), [6] (Harris-Fry *et al.* 2015), [7] (Bashir, Schilizzi & Pandit 2012), [8] (Baulch and McCulloch 1998), [9] (Mutisya *et al.* 2016), [10] (Duarte, Sampaio & Sampaio 2009), [11] (Machado & Neto 2016), [12] (Endo, Peres & Haugaasen 2016), [13] (Cinner *et al.* 2016), [14-15] (Geheb & Binns 1997; Watson *et al.* 2013), [16] (Brashares *et al.* 2004), [17-18] (Wilkie & Godoy 2001; de Jesus Silva *et al.* 2016)

3.3. Methods

3.3.1. Study area

The study was carried out in rural river *ribeirinho* communities along the River Purus in the Brazilian Amazon (Fig. 3.1). The river offered a unique system to study how seasonal changes interact with overfishing in an otherwise relatively pristine environment. The River Purus supplies more fish to the Amazon's largest city, Manaus (population 2.1 million people; IBGE, 2010), than any other river (Batista & Petrere Júnior 2003; Cardoso *et al.* 2004; Gandra 2010), demand from which has been blamed for the overfishing of the commercially important tambaqui (*Colossoma macropomum*) in the river (Chapter 2). However apart from overfishing, it does not suffer significantly from the other major threats of Amazonian freshwater degradation; deforestation, pollution and dam construction (Castello *et al.* 2013). The Purus River catchment meets the definition of a wilderness area (Mittermeier *et al.* 1998), with high remaining forest cover, and low human population densities (Table 1.2). It is the only major Amazonian tributary whose watershed remains undammed, and one of three with an undammed main channel (Winemiller *et al.* 2016).

Fig. 3.1. Floodplain map of the study area.



The Purus is an ideal system to study the impact of the seasonal flood pulse, as it sees some of the highest seasonal amplitudes in river levels in the Amazon Basin (Castello & Macedo 2016), transforming much of the catchment into *várzea* flooded forest (Fig. 3.1). The seasonal flood pulse has an enormous impact on aquatic and terrestrial ecology and the activities of the local people in the Amazonian floodplain. Data were collected during a high water (April – July 2014) and a low water (August – November 2014) field season. This also avoided working during the *defeso* fishing closed season, thereby avoiding unnecessary variation in fishing activity or the reporting of it. We descended the River Purus to accompany the rising and falling water levels, with the intention of visiting each community at approximately the peak and trough of annual water levels. In order to achieve this, we planned the timing of the journeys on the river-level calendar based on long-term averages (Coe *et al.* 2002).

3.3.2. Sampling

We worked downstream of the town of Lábrea and upstream from the confluence with the River Solimões. From the first to the last community the fluvial travel distance along the River Purus was 1267 km, as calculated using the travel network function in ArcGIS 10.2.2 (ESRI 2014). We would stop at the first community we came to as we travelled downstream from Lábrea that had at least 10 ordinarily (not necessarily currently) inhabited houses, ignoring larger communities (>31 houses). In order to maximise the distance covered and maintain spacing between communities, we would not stop at another community for a minimum of 13 km (mean 61 km) fluvial travel distance after leaving the last one. We did not work in the stretch of the river covered by the Abufari Biological Reserve, as regulation and monitoring concerning harvesting practices were much more intense than in sustainable use reserves or unprotected areas, potentially causing unnecessary variation in results; both ecological, and in terms of response-bias.

An unexpected challenge of sampling was encountered in several communities that were partially or fully abandoned at high water, which for some people was an ordinary annual routine (many people go to houses on the *terra firme* '*por centro*' deeper in the forest during ordinary floods (Winklerprins 1992)), or because other people had abandoned their flooded houses as 2014 brought exceptionally high waters (Espinoza *et al.* 2014). Communities entirely abandoned at the time of encounter at high water were visited neither at high nor low water.

We visited a maximum of 20 households per community. Where a community had more than 20 households, we would ask the village president (or another representative where absent) for the name of the head of each household, which they would then select randomly in a lottery system. Within each household we asked how many times each individual household member had gone fishing and hunting in the past 30 days (whether successful or not), excluding occasions where someone had gone just to help out (e.g. just paddling the canoe). We interviewed every household member of 16 years of age or older (referred to as an adult hereafter) that had been fishing or hunting in the past 30 days, hereon referred to as fisher and hunter respectively, or harvesters collectively. Interviews were used to collect social and ecological data from sampled households and people, concerning food insecurity, domestic meat consumption, and fishing and hunting activities.

3.3.3. Fishing and hunting data

Ecological studies are increasingly utilising interviews to gain important knowledge (Thurstan *et al.* 2015), including the recording of catch, effort and CPUE data. Commercial CPUE is probably the most widely used index of abundance in marine fisheries, particularly in data poor situations (Edwards *et al.* 2012). CPUE is now commonly used in studies of bushmeat hunting (Parry, Barlow & Peres 2009; Rist *et al.* 2010; Gill *et al.* 2012) and tropical inland fisheries (Almeida, Lorenzen & Mcgrath 2002; Hallwass *et al.* 2011; Pinho, Orlove & Lubell 2012), in which remoteness and low observation rates impede data collection. Collecting data on harvester catch and effort has been shown to be much cheaper and more efficient than traditional methods, yet with similar levels of accuracy and precision for estimating CPUE (Rist *et al.* 2010; Thurstan *et al.* 2015).

To keep response variables spatially associated with the community's location, we restricted information to harvesting trips that had occurred within 2 hours motorised canoe (*rabeta*) journey from the harvester's home in the community. Pilot studies suggested that two hours of travel time was a measure that local people could easily relate to, with the additional advantage of being fairly standard as almost all harvesting was undertaken using motorised canoes of similar power (generally 5.5 horse-power) that travel at around 9 km h^{-1} (Parry 2009).

All fishers were asked in detail about the catch, effort and catch methods of every fishing trip (whether successful or not) that they had undertaken in the 72 hours prior to the interview. For catch, respondents were asked to identify every animal caught (to species level where possible), and how many individuals of that taxa they had caught. These catch data were converted to biomass using additional standard species weights we collected along the Purus. Fish catch was calculated as the sum of the biomass of all the fish caught per catch, or of all the catches summed per household (depending on the analysis).

Our pilot study confirmed previous work (Pinho, Orlove & Lubell 2012) that states that where fish are sold directly by the fisher per unit weight, the fisher can estimate biomass of these species accurately. In our study system this was the case for larger species (those that commonly weighed >1kg), namely the large catfish (surubim *Pseudoplatystoma fasciatum*, pirarara *Phractocephalus hemioliopterus*, caparari *Pseudoplatystoma tigrinum*, filhote *Brachyplatystoma filamentosum* and jaú *Zungaro zungaro*), pirarucu *Arapaima gigas*, tambaqui *Colossoma macropomum*, aruanã *Osteoglossum bicirrhosum* and pirapitinga *Piaractus brachypomus*), which were commonly sold species, and priced per kilogram. In the few cases that these estimates were missing (rarely, fishers felt unable to estimate) a mean of all other estimates of the relevant species weight was used. Smaller species were however commonly fished for subsistence or sold per individual, and fishers found estimating biomass of these species more challenging during the pilot study, so we therefore did not rely on fisher biomass estimates for these species, and instead calculated catches using standard species weights.

While maximum species weights can be derived from FishBase (Froese & Pauly 2015), we wanted to accurately represent landed species weights. This was challenging to obtain in the field because we required the average weight that was caught and landed by a local fisher as uninfluenced by the researcher, and hence we were unable to weigh (a) fish caught by ourselves, or (b) fish that we asked a fisher to catch for us. We therefore opportunistically weighed 1515 fish individuals of 78 species (plus 2 genera, not identified to species level) that were caught and landed by local fishers, uninfluenced by the researcher. A mean weight per species was used in analyses for those weighed, however where weights lacked for certain rarer species, we calculated mean landed weight. We calculated the maximum species weight by inputting maximum lengths and relevant coefficients from FishBase (Froese & Pauly 2015) into the fish weight-length equation. We then calculated how much smaller the fish landed by Purus fishers were than maximum sized fish from the literature (Santos, Ferreira & Zuanon 2006; Froese & Pauly 2015), finding that the mean landed fish was 60-89% (reduction factor) of the maximum species weight. Reducing the maximum species weight by the calculated reduction factor of the closest related species possible where FishBase data was available, gave us our estimates of mean landed weights for each species. The overall weight of fish caught in each harvesting trip (past 72 hours) was calculated by multiplying the number of individuals caught of a particular fish species by the standard tabulated mass for that species.

Biological fishing effort (the time spent fishing, but not travelling to the fishing grounds) in minutes was calculated as the time the fisher spent away from their house, minus the return travel journey time, which was excluded to enable measurement of fish catch rate in the local aquatic environment. Where a fishing net was used we asked the mesh size (distance in mm of the mesh between opposite knots (Batista 2006)), length (normally a standard manufactured piece, which is 100m outstretched, or 70.72m once threaded; i.e. how it is deployed in the water), and the height (a standard manufactured piece is 48-50 meshes high, which was converted into metres). The length and height were used to calculate the net area. Accumulated CPUEb was simply calculated as catch (kg) divided by effort (hours fishing). Net specific CPUEb (kg (m^2 hour)$^{-1}$) was calculated by dividing catch by net area (m^2) multiplied by effort.

As with fishing surveys, the detailed hunting surveys also collected data on the past 72 hours harvesting activity. However, there were too few hunting events reported in this time period to use this data in this study. We therefore used hunting recall data from the 30 days prior to interview, which only included the species (or broader taxon where unidentifiable) and quantity hunted. We generated total hunted biomass figures by using published species body weights to estimate and sum the biomass of each individual hunted (Table S3.1).

3.3.4. Food insecurity

We aimed to measure household perceptions of food insecurity and initially considered using the Brazilian Household Food Insecurity Scale (EBIA; IBGE 2010). However, after consideration we decided that the EBIA was unsuitable due to the strong focus on food purchase, which is of secondary importance to a population that fishes most of their protein and plants most of their calories (Murrieta and Dufour 2004; personal observation). Instead, we measured perceptions of food insecurity quantitatively based on the frequency and severity of locally-defined coping strategies, based on work by Maxwell (1996) and Maxwell et al. (1999). Focus groups were undertaken prior to interviews in several communities along the river in order to determine what coping strategies *ribeirinhos* use in times of food scarcity. We then took the most common responses to these focus groups and transformed them into the following questions that were then asked to a representative of each household during both the high and low water seasons.

In the last 30 days has anyone in the house:

1. Gone the whole day without eating anything (having just a *merenda* snack was included as eating nothing, which often comprised of just coffee and crackers)
2. Gone the whole day without eating any fish or meat (wild or farmed)
3. Skipped lunch or dinner at home (if they skipped a meal while harvesting or undertaking other work in the field this was not included, as it is common due to impracticalities or unexpected delays)
4. Eaten only *farinha* (manioc flour) for lunch or dinner at home (known as *chibé* or *jacuba,* this dish is generally despised, but not uncommonly eaten when working in the field for convenience; it consists only of *farinha*, water and either salt or sugar)
5. Had to eat less fish or meat than they would have liked to at lunch or dinner
6. Substituted fish or meat with an alternative protein source such as eggs, beans, tinned meat or fish, or sausages

It was stressed that these questions related to activities taking place in the home. Undertaking such activities in another person's house, or in the field (e.g. whilst fishing) would have little relation to the food security of that household. Due to the difficulty in recalling the exact frequency that coping strategies were undertaken in the past 30 days exactly, and in accordance with methodology undertaken by Maxwell et al. (1999), we pooled frequencies into five categories: never, less than once a week, 2-3 times a week, 3-6 times a week, or every day.

3.3.5. Domestic meat consumption

Due to the growing importance of domestic meats as part of the 'nutrition transition' within *ribeirinho* populations (van Vliet *et al.* 2015a), we measured the frequency of consumption of chicken and beef by asking a representative from every household how many times they had been consumed within the household in the past 30 days. We used the same frequency categories as with the food insecurity scale. We also asked about the origin of the meat consumed in order to determine the relative importance of community-reared livestock and purchased imported industrialised meats. Where chicken had been consumed we asked if it was frozen, home reared, or from a local farm. Where beef had been consumed we asked if it was killed within or outside of the community. We estimated total household chicken consumption assuming that a household consumes one whole chicken per consumption event, using 2.2 kg as the mean weight of a slaughtered chicken in Brazil (IBGE 2016).

3.3.6. Statistical Analysis

Statistical analyses were performed in R statistical software version 3.1.3 (R Core Team 2015). Linear mixed-effects models (LMMs) with community as the random variable were used to perform multivariate analyses (lme4 package in R). For analyses at the level of fishing trips and households, fisher and household identification were used, respectively, as additional random factors. Model diagnostic plots were subsequently inspected. P-values were calculated using likelihood ratio tests. Models testing seasonal and spatial variation used season (high or low water), and fluvial travel distance from Manaus and the closest town as fixed explanatory variables. To test the probability of fishing or hunting, we used LMMs. Due to the high number of households with zero hunt catch, and that did not fish at all in the previous 72 hours, we used a zero-inflated GLMM (general linear mixed-effect model) with community as a random factor to test for trends in the *glmmADMB* package.

Models testing intra-community variation used travel distance to Manaus and the nearest town as fixed explanatory variables, in addition to house type (*flutuante* floating house or a land house on stilts), years of education, household population size, floor area of the house (an indicator of wealth), the proportion of the household that are classed as dependents (children <16, and elderly >59 years of age), and a variable factoring in dependence and conditional cash transfers (*Bolsa Familia* or pensions). This final variable that considered dependence split households into three categories: (1) in which nobody in the house was eligible for benefits by age (no children <16, females >54, and males >59), (2) where the household contained at least one eligible person, and received at least one government payment, and (3) where the household contained at least one eligible person, but received no government payment. To assess the relative importance of household variables in explaining food insecurity, we used the dredge function to compare AIC (Akaike's information criterion) values, considering those with a delta-AIC of less than 2 as plausible models (Dziak *et al.* 2012).

3.3.7. Ethics

Our research proposal was assessed and approved by ethics councils in both Lancaster University (United Kingdom) and the Federal University of Lavras (Brazil). Article 37 of Brazilian law 9605 from 1998 states that killing an animal is not a crime when it is carried out to satisfy the hunger of the harvester or their family. As we intentionally do not specify which fishing and hunting activity was commercial, we do not associate any person or community with illegal activities in order to maintain anonymity.

3.4. Results

We visited 22 communities along the River Purus during the peak of both the high and low water seasons. We visited 331 different households, 270 in the high water season and 296 in the low water season (566 household visits in total), from all of which visits we collected household food insecurity and domestic meat consumption data. During all household visits we asked whether each adult household-member had fished and/or hunted in the high water season (n = 700 interviews) and low water season (n = 766 interviews). In the high water season 69.9 % of interviewees had fished and 14.7 % had hunted, compared to 53.9 % fishing and 5.9 % hunting in the low water season. We collected data on 886 fishing trips undertaken in the 72 hours prior to interview by 385 different fishers in the high water (n = 517 trips) and low water (n = 369 trips) season. We calculate that households catch (adults only) an average of 5506.5 ± 1590.6 g of fish and 271.2 ± 69.8 g of bushmeat, and consume an average of 174.6 ± 8.6 g of chicken per day.

3.4.1. The spatial and temporal drivers of rural food insecurity

Our hypothesis that food insecurity would be greater in the high water season was strongly supported by the data. The cumulative food insecurity index showed that households were significantly more food insecure in the high water season ($P < 0.001$, $n = 561$, Fig. 3.2A). When analysed by frequency of individual (unweighted) coping strategy we found five of the six coping strategies were undertaken significantly more frequently in the high water than the low water season (Table 3.2). There was consensus about the order of severity of the six coping strategies amongst the focus group participants. In order of least to most severe they were to: (i) eat something else instead of fish or meat, (ii) not eat any fish or meat for a whole day, (iii) skip lunch or dinner, (iv) reduce the quantity of fish or meat consumed, (v) eat only toasted manioc flour with salt and water (*chibé*), and (vi) eat nothing all day.

Fig. 3.2. Food insecurity and fishing activity in the high water season (blue) and low water (red) season. Boxplots showing seasonal comparisons of (A) household food insecurity (weighted score), (B) fish catch rate (CPUEb; (log kg hour^{-1})) per trip, (C) household fish catch (kg caught within previous 72 hours by all adult household members), (D) household fishing effort (hours of spent fishing by all adult household members). Individual data points are jittered. Seasonal differences between all four variables were tested with LMMs, and all were significant to P < 0.001 level.

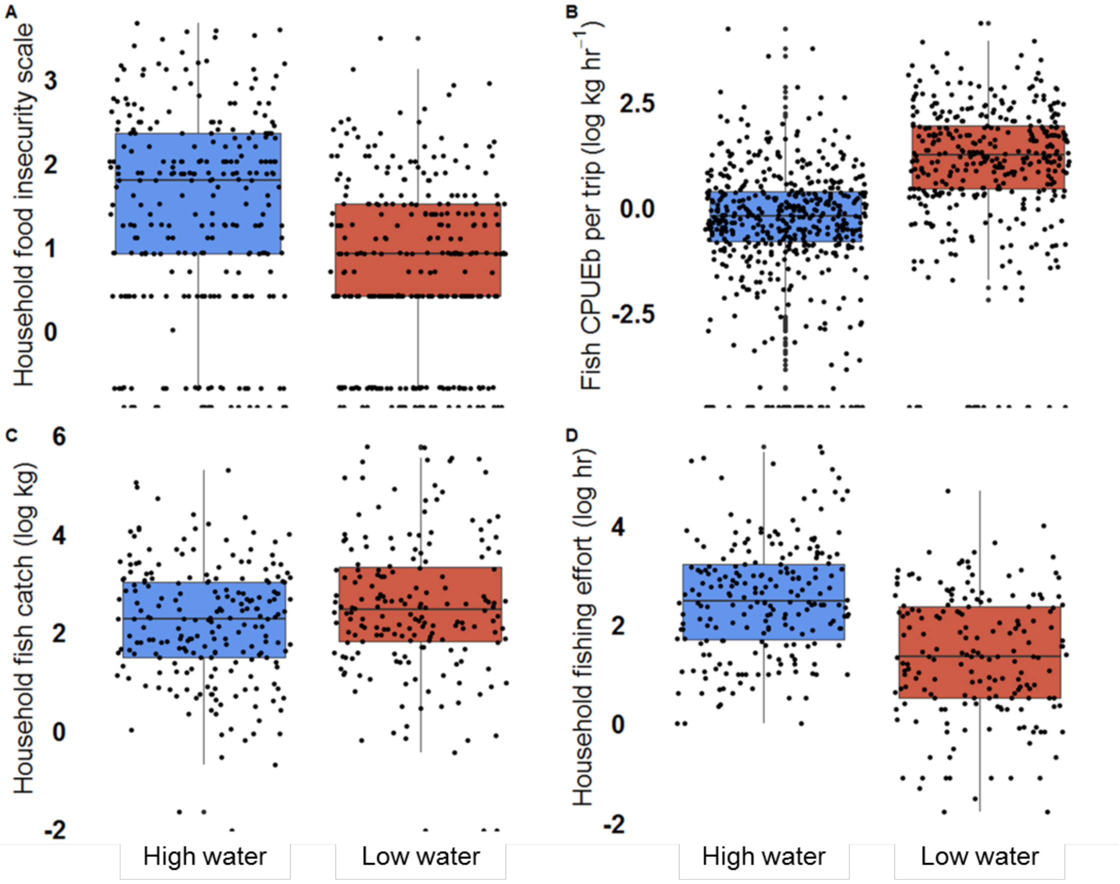


Table 2. Food insecurity model results. Results of linear mixed models for the household food insecurity index, and the frequency of the six individual food insecurity coping strategies. The coping strategies are listed in order of decreasing severity as perceived by focus group participants. All statements were asked about coping strategies undertaken in the 30 days prior to interview by anyone living in the household. Distance to Manaus and distance to the nearest town variables divided by 100, thus any deductions should be made per 100km. N = 565 household interviews from 331 different households.

		Distance to Manaus		Distance to nearest town		Seasons		Mean weekly frequency	
Food insecurity index	Severity	Coefficients & SE	z	Coefficients & SE	z	Coefficients & SE	z	High water	Low water
Accumulated index	NA	-0.022(0.020) NS	-1.06	0.002(0.105) NS	0.02	-0.880(0.022)***	-40.08	NA	NA
To eat something else instead of fish or meat	Least	-0.018(0.014) NS	-1.30	-0.077(0.073) NS	-1.06	-0.179(0.041)***	-4.36	1.27	1.07
To not eat any fish or meat for a whole day	↓	-0.123(0.036)***	-3.45	-0.048(0.177) NS	-0.27	-0.973(0.106)***	-9.15	0.31	0.14
To skip lunch or dinner		-0.112(0.043)*	-2.59	0.294(0.220) NS	1.34	-0.683(0.083)***	-8.23	0.43	0.22
To reduce the quantity of fish or meat consumed		0.014(0.021) NS	0.68	-0.017(0.108) NS	-0.16	-1.329(0.076)***	-17.43	0.79	0.23
To eat *farinha* with salt/sugar and water		-0.007(0.108) NS	-0.07	-0.267(0.612) NS	-0.44	-0.413(0.269) NS	-1.54	0.04	0.04
To eat nothing all day	Most	-0.073(0.072) NS	-1.02	0.182(0.359) NS	0.51	-1.321(0.201)***	-6.58	0.12	0.03

*P < 0.05; **P < 0.01; ***P < 0.001; #P < 0.1; NS, not significant

This study does not provide evidence of spatial trends in food insecurity, which we hypothesised to increase with proximity to urban centres. Based on the cumulative index, food insecurity was not significantly influenced by distance to Manaus ($P = 0.30$), or the nearest town ($P = 0.98$). However, the frequency of two of the individual coping strategies were significantly more common near Manaus: to not eat any fish or meat for a whole day ($P < 0.001$) and to skip lunch or dinner ($P = 0.016$). No significant trends were found with distance to the nearest town.

3.4.2. Household vulnerability to food insecurity

Our data supports the hypotheses that wealthier households with fewer residents would suffer least from food insecurity. Floor area and household population were found in all of the best approximating LMMs (Table 3.3), whereby food insecurity was more severe in households that were smaller in floor area, and with larger household population sizes. Other variables that appeared in models and had a positive relationship with food insecurity were distance to Manaus and the proportion of the household that was dependent (i.e. not 16-59 years old). Years of education appeared in several models and had a negative trend with food insecurity. Food insecurity was greater in floating houses (*flutuantes*) than in houses on land.

Table 3.3. Important household predictors of lean season food insecurity in descending order of model plausibility. The seven best approximating linear mixed-effects models (ΔAICc < 2 from top-ranked model) determining food insecurity in the high water season, with associated AIC (Akaike's information criterion) values. Other predictor variables were distance to the nearest town and a variable factoring in dependence and conditional cash transfers (*Bolsa Familia* or pensions). ΔAICc is the difference between AICc of the top-ranked and current model.

Explanatory variables	AICc	ΔAICc
~ floor area + household size	1689.4	0.00
~ floor area + household size + education	1689.6	0.24
~ floor area + household size + house type	1690.7	1.33
~ floor area + household size + proportion dependent	1691.0	1.57
~ floor area + household size + education + house type	1691.2	1.78
~ floor area + household size + education + proportion dependent	1691.3	1.87
~ floor area + household size + distance to Manaus	1691.3	1.94

3.4.3. The importance of fish catch rate in driving food insecurity

Our data supports the hypothesis that fish catch and catch rate drives the significant seasonal variation in food insecurity. A major finding was that mean fish catch rate (CPUEb) per fishing trip was 73 % lower in the high water season (mean = 1.55 ± 0.2 kg hr^{-1}) than in the low water season (mean = 5.73 ± 0.4 kg hr^{-1}; $P < 0.001$) when aggregated by all fishing gears (Fig. 3.2B). For those gear types used regularly in both seasons (Fig. S3.1; ≥ 8% of trips per season), mean fish catch rate using gill nets was 96 % lower in the high water season than the low water season ($P < 0.001$; mean 0.33 and 8.09 kg 100 m^{-2} hr^{-1} respectively (Fig. S3.2)), and 72 % lower with hooks on rods or hand-lines ($P < 0.001$; high water: mean = 1.37 and 4.85 kg hr^{-1} respectively (Fig. S3.3). Fishing trips that landed no catch at all were 37 % less likely in the low water season (4.6 % of trips) ($P = 0.047$, $n = 886$) than the high water season (7.4 % of trips), despite lasting 58 % less time (mean of 5.8 and 13.9 hours), although not significantly ($P = 0.75$, $n = 55$). Travel distance to Manaus or the nearest town respectively did not significantly affect overall fish catch rate for all gear types ($P = 0.815$ or 0.767), or when split into gillnets ($P = 0.198$ or 0.283) or hooks ($P = 0.685$ or 0.666).

The mean biomass of fish caught per household in the 72 hours prior to interview in the high water season (16.90 kg) was approximately half of that in the low water season (32.12 kg, $P < 0.001$, Fig. 3.2C). There was no significant trend found in biomass caught per household with distance to Manaus ($P = 0.73$) or distance from the nearest town ($P = 0.99$).

3.4.4. Responses to low fish catch rate

Analyses support the hypothesis that harvesting effort increases in response to seasonally low fish catch rate. Households spent 2.6 times longer fishing (biological fishing effort in previous 72 hours) in the high water season (mean = 10.20 hrs) than the low water season (mean = 3.88 hrs) ($P < 0.001$, $n = 780$, Fig. 3.2D). In the high water season around two-thirds (69.9 %) of adults had fished in the past 30 days, compared to around half (53.9%) in the low water season ($P < 0.001$, $n = 1466$). There was no significant trend found in fishing effort per household with distance to Manaus ($P = 0.83$) or distance from the nearest town ($P = 0.41$). Adult participation in fishing was more common farther from Manaus ($P < 0.001$, $n = 1466$), but was unrelated to distance from the nearest town ($P = 0.13$).

Fishing strategies varied seasonally, and although gill nets were common in both the high water (43.7 %) and low water (52.0 %) seasons, hooks were mainly used in the high water season (52.2 %), while cast nets were employed more in the low water season (35.2%; Fig. S3.1). In terms of habitat, almost all fishing was undertaken in the *várzea* flooded forest in the high water season (90.0%), and mainly in the river channel (76.3 %) and lakes (20.3 %) during the low water season (Fig. S3.4).

Harvesting at least some bushmeat in the previous 30 days was over twice as likely during the high water season (20.7% of households) than the low water season (8.1 %) (P < 0.001, n = 566), whereas distance to Manaus or local town were not significant. Chicken had been eaten once every 13 days and in the majority of households (67.3%) in the previous 30 days, while beef had been eaten once a month and in the minority (27.2%). However, there was no significant difference in the frequency of chicken (P = 0.119, n = 566) or beef (P = 0.123, n = 566) consumption between seasons. Significant spatial trends were found in the consumption of domestic meats, with chicken consumption being more frequent nearer small towns (P = 0.007; Fig. 3.3A) and nearer Manaus (P = 0.0027; Fig. 3.3B), and beef consumption more frequent nearer small towns (P < 0.001; Fig. 3.4C).

Fig. 3.3. Spatial relationships in domestic meat consumption. The relationship between household consumption frequency of (A) chicken and fluvial travel distance to the nearest town and (B) Manaus, and (C) beef and fluvial travel distance to the nearest town and (D) Manaus, split by season. The vertical red dotted line on figs. B and D represent the limit of Manaus-based ferry boats that buy fish, sell domestic meat, and deposit ice

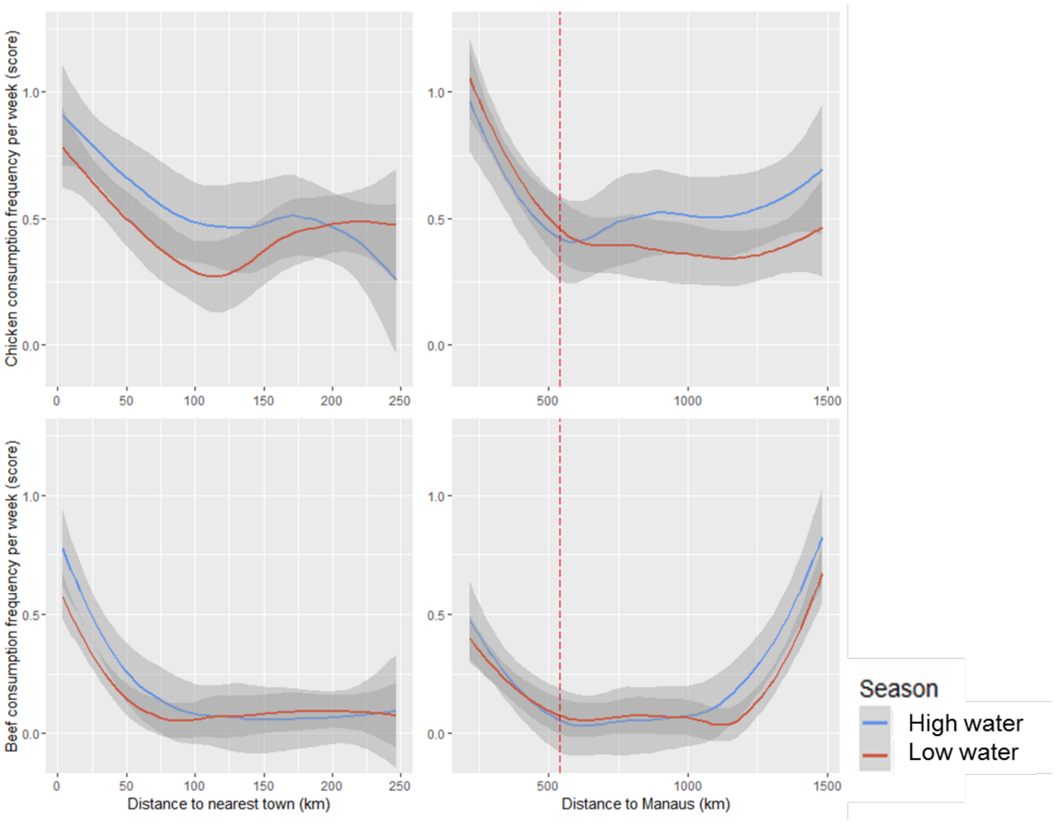
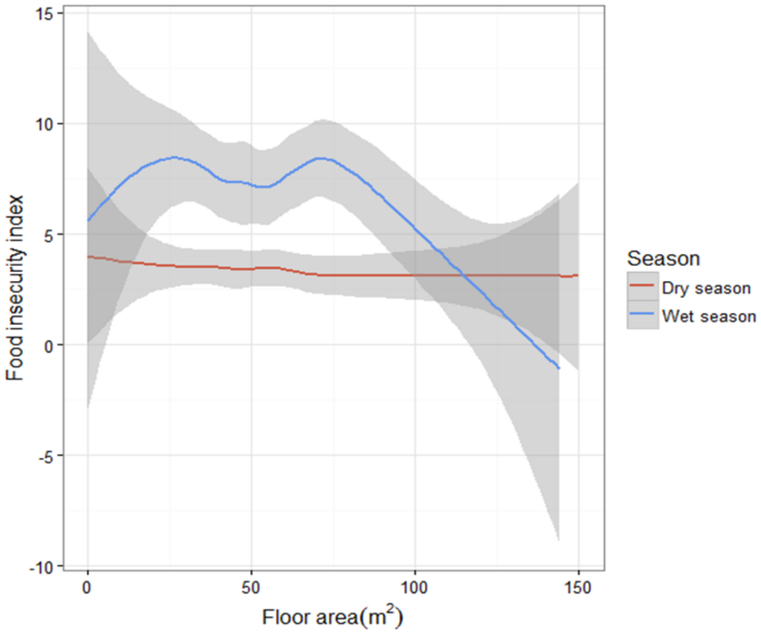


Fig. 3.4. The relationship between household floor area (proxy for wealth) and food insecurity in the high water and low water seasons.



3.5. Discussion

We present the first empirical evidence that seasonal food insecurity among rural households is associated with lower wildlife catch rates. In our study of Amazonian river-dwellers this occurs in the high water season as we hypothesised. Given the great reliance of *ribeirinhos* on fish as a main source of protein, and important source of fats, energy and micronutrients, a reduced catch rate and thus catch can have important consequences for their food security and health. As hypothesised, we found that although households respond to resource scarcity in the high water season by fishing and hunting more often and for longer, they are unable to maintain harvest levels. An additional important finding that goes against hypothesised spatial trends was that neither fish catch rate nor food insecurity is significantly related to distance from a metropolitan centre or local towns, and appears that Amazonian fishers are able to maintain catch-rate and food security along a commercially overfished spatial gradient. Our observations strongly support the hypothesis that declines in fish catch rate drives food insecurity in our study system. However, despite evidence of defaunation of a key fish species (Chapter 2) and of mammalian populations (Parry & Peres 2015) in or around the floodplain, there is no concomitant evidence that this is explicitly linked to food insecurity. Our results also highlight social inequalities because ostensibly less-poor households are buffered from the food insecurity impacts of the lean season, and households with smaller population sizes suffer less. Lastly, the fact that chicken and beef were eaten so rarely in most rural areas, and even during the flood period when fish is hard to come by, is evidence that they may make a less significant impact to food security than the literature suggests.

3.5.1. Evaluating the spatial and temporal drivers of rural food insecurity

Our data strongly support the hypothesis that seasonality drives food insecurity in rural Amazonia. This adds to previous studies from developing countries that reported seasonal food insecurity during lean food production seasons, indicated by perceptions of food insecurity or physical problems such as wasting and stunting (Ferro-luzzi *et al.* 2001; Hillbruner & Egan 2008). The identification of seasonal food insecurity among rural Amazonians living in the floodplain population is important. Seasonal food insecurity is a largely neglected form of food insecurity relative to the research and policy attention to the impacts of exogenous shocks (Chambers 2012), yet which is thought to be the most common form (Vaitla, Devereux & Swan 2009; Barrett 2010). The prevalence of food insecurity may seem paradoxical for inhabitants of relatively intact (94.8 - 99.6 % forest cover in our studied municipalities) flooded forest rich in natural resources, and living at such low human population densities (0.22 - 0.89 people per km^2 in our studied municipalities; Table 1.2). Yet food insecurity in our study system can be considered severe; evidenced by high rates of malnutrition among rural Amazonians (Alencar et al. 2007, 2008; Piperata 2007; Piperata et al. 2013), and the relative severity the coping strategies that they undertake (Table 3.2) in relation to the FAO's definition of the food insecurity severity. Along a continuous scale, they describe food insecurity severity, from mild to severe, as: (1) worrying about how to procure food, (2) compromising on quality and variety, (3) reducing quantities, skipping meals, (4) experiencing hunger (Ballard, Kepple & Cafiero 2013), and our study therefore provides evidence of the three more severe forms of food insecurity.

Recognition of seasonal threats is important in a population so highly dependent on its seasonally-transformed landscapes and natural resources, and vulnerable to malnutrition as a result of several non-food factors. Poor sanitation and healthcare access in rural Amazonia, which results in the high incidence of gastroenterological infections and ultimately iron anaemia, means that a dietary loss of essential nutrients may become critical at peaks of food insecurity when the ability to replenish them is limited. These malnutrition issues become particularly relevant in a population with high levels of malaria, a disease that is highly aggravated by the presence of anaemia (Quintero *et al.* 2011). The food insecurity identified during the high water season is therefore not trivial, and must be placed in context of the susceptibility of the general population, principally those individuals and households whose specific social circumstances make them particularly vulnerable.

Despite the strong temporal trends in food security, we found no evidence to support our hypothesis that food insecurity would be greater with increasing proximity to urban areas. This hypothesis was based on evidence of overfishing nearer Manaus (Chapter 2), which we predicted would be positively related to CPUEb. The lack of food insecurity trend may therefore be explained by the lack of CPUE trend, which will be discussed in more detail later.

3.5.2. Household vulnerability to food insecurity

Modelling the household-scale predictors of high water season food insecurity highlighted two clear explanatory variables: deprivation (contended to be inversely related to house floor area) and household population size. The relationship between deprivation and food insecurity reveals that only the wealthiest minority of households avoid food insecurity in the high water season (Fig. 3.4). That wealth does not affect food insecurity during the low water season further supports our conclusion that seasonality is the principal factor determining food insecurity in our study system. This is counter to widespread claims of the high importance of purchased food and the 'nutrition transition' in *ribeirinho* diets security (Nardoto *et al.* 2011; van Vliet *et al.* 2015a; de Jesus Silva *et al.* 2016).

Despite low mean frequency of implementation of the coping strategies, particularly the more severe ones, the impacts are not even within communities, and so the averages are deceptive. For large families living in small houses, in the high water season our data suggest they are regularly missing meals. This is despite labour intensive, tiring lifestyles, and this could have quite serious developmental consequences for the children brought up in these households.

Past work has shown that wealth is closely linked to household food insecurity (Bashir, Schilizzi & Pandit 2012; Harris-Fry *et al.* 2015), which is consistent with our findings although our results show that relationship may be present during the lean period of the year and absent during the period of high wildlife abundance. An increased income specifically during the lean season has been shown to improve food security, particular in terms of increased animal protein, and even nutritional status of food insecure women and children (Mascie-Taylor *et al.* 2010). However, improved financial capabilities (wealth or income) do not always have a positive effect on food security, and has even been shown to impact negatively (Morris *et al.* 2004). In *ribeirinho* communities, the increase in cash largely due to the growth in conditional cash transfers has resulted in a rise in the consumption of less nutritionally valuable industrialised meats such as processed sausages, and tinned-beef (van Vliet *et al.* 2015a), in what Piperata et al. (2011) describes as the '*efeito mortadela*' (mortadella effect).

3.5.3. The importance of fish catch rate in driving food insecurity

Our evidence shows that in the high water season rural Amazonians tend to encounter far lower CPUEb of fish (370 % greater in the low water season) – their principal form of animal protein (Murrieta & Dufour 2004; van Vliet *et al.* 2015a; Endo, Peres & Haugaasen 2016; Dufour *et al.* 2016) – and far higher levels of food insecurity. The importance of fish-catch rate is clear because household fish catch exceeded bushmeat catch and chicken consumption by more than an order of magnitude. In the low water season, when fish were abundant and easy to catch, the deprivation-food insecurity linkage was broken, further indicating the relatively predominance of fish in Amazonian diets. Moreover, the mutual lack of spatial relationships in either food insecurity or fish catch rate further supports our hypothesis. Fish catch rate therefore appears to be a key driver of the seasonal variation observed in food insecurity. Low fish catch rate in the high-water season has been observed in other studies in systems with seasonal flood-pulses (Begossi *et al.* 1999; Da Silva & Begossi 2009; Poulsen *et al.* 2009; Endo, Peres & Haugaasen 2016), because the relative abundance (density) of fish is lower when water volume is greater (Saint-Paul, Zuanon & Correa 2000).

Contrary to our hypothesis, fish catch rate was not lower nearer Manaus or small towns, despite overharvesting of a key fish species in these areas (Chapter 2). This may either be due to the difficulty in detecting biomass declines in overfished tropical mixed fisheries caused by CPUE hyperstability, or because biomass did not vary spatially as a result of density compensation. Hyperstability explains how CPUEb can be maintained in areas of reduced biomass as a result of human and fish behaviour, whereby fish may shoal more densely as numbers dwindle, and how fishers have centuries of knowledge about when and where to find remaining shoals (Erisman *et al.* 2011; Castello, Mcgrath & Beck 2011; Hamilton *et al.* 2016). However, density compensation explains how overfishing may not even impact the cumulative fish community biomass (MacArthur, Diamond & Karr 1972; Allan *et al.* 2005). Commercial overfishing commonly targets larger species and individuals, which are often preferred by harvesters (higher return on effort) and consumers alike, as well as being the more vulnerable members of the community due to their slow growing nature and large range sizes. As such, larger fish are often the first to be lost from an overfished community (Allan et al. 2005; Chapter 2). Environmental resource use is generally high for larger fish, in the form of consumption of primary producers (plants and algae), invertebrates, or other fish because larger fish species are often piscivorous or even top apex predators (Allan *et al.* 2005). Density compensation explains how the selective defaunation of large fish from a community frees up resources for other fish, and release smaller fish from predation pressure (Lorenzen & Almeida 2006). A commercially overfished tropical mixed fishery is therefore often characterised by a community that has lost many of its larger commercially-desired fish, which have been replaced by smaller undesired fish, thereby potentially maintaining community biomass.

Density compensation and hyperstability are commonly ignored, instead leading some to interpret signs of overfishing as evidence of reduced fish community catch rate, and therefore food security of fishery-reliant populations (Golden *et al.* 2011; Castello *et al.* 2013; Parry & Peres 2015). In this study, spatial overfishing (evident by the collapse of the tambaqui fishery; Chapter 2) did not result in a decline in community fishing CPUEb or food insecurity. Evidence suggests that globally, people dependent on wildlife for food can be adaptable to changing prey availability, and as much as some populations increase focus on bushmeat when overall fish catch rate is low (Midorikawa *et al.* 2003; Brashares *et al.* 2004; Poulsen *et al.* 2009; Endo, Peres & Haugaasen 2016), some also focus on different fish species when the availability of preferred species is low (Pauly *et al.* 1998; Newton, Endo & Peres 2011). We therefore argue that the impacts of commercial overfishing on food security may be over-estimated due to density dependence or hyperstability. However, it is important to note that more extreme overfishing can deplete even small fishes, and therefore reduce cumulative community biomass, particularly in areas of high fishing pressure, and in less productive systems than the River Purus such as oligotrophic waters. Moreover, other anthropogenic impacts such as dams are reducing Amazonian river productivity and fish abundance, and therefore catch rate (Carolsfeld *et al.* 2003; Winemiller *et al.* 2016). These may also have a negative impact on food security, and may result in greater pressure on terrestrial fauna, as a form of compensation (Brashares *et al.* 2004; Endo, Peres & Haugaasen 2016).

Although we show no evidence that overfishing results in food insecurity, livelihood security may suffer from commercial overfishing, through the loss of larger fish species and size classes. These fish tend to be more commercially valuable, and the larger individuals are often the only selection of some species that can be legally sold due to minimum size restrictions (de Almeida Corrêa, Kahn & Freitas 2014). This is important as the main source of earned income for most households in the study area is fishing (Fig. S2.5), and as increased environmental restrictions on natural resource extraction has already reduced livelihood options for Amazonians. Therefore while some form of fisheries management is essential to prevent the further decline in aquatic species, the options available to river-dwelling Amazonians to earn a livelihood have become somewhat limited in recent decades (e.g. loss of profitability of rubber tapping, and regulations preventing logging and wildlife pelts), which may explain widespread depopulation of remote rural areas (Parry *et al.* 2010a).

3.5.4. Responses to low fish catch rate

We found that rural people responded to lower fish catch rate in the high-water season by increasing their fishing and hunting effort, adopting different fishing techniques (mainly hooks), and fishing in different habitats (mainly the shallower waters of the *várzea* flooded forest). Contrary to our hypothesis however, we observed no seasonal differences in domestic meat consumption, which was consumed rarely. By changing fishing techniques and increasing effort, overall fish catch in the high-water season was only 47 % lower, despite a 73 % reduction in catch rate. Other studies show that fishers are able to maintain or even increase catch despite CPUE declines. An increase in effort is a common response to falling fish stocks, which for example has resulted in an increase catch in the severely depleted international marine fishery over decades, despite a steadily falling CPUE (Watson *et al.* 2013). Furthermore, in the long term, huge technological advances in fishing vessels, navigation, fish capture and refrigeration have occurred in most fishing systems (Roberts 2007), including Amazonia (Mcgrath 1989), which have maintained the high catch of dwindling stocks (CPUE).

Although fish is the main protein source for people living in the Amazonian floodplain, probably largely as a result of the comparative reliability of capture in comparison with bushmeat (Endo, Peres & Haugaasen 2016), hunting becomes a relatively efficient option when fishing is difficult (lower fish CPUE). Long-term evidence from West Africa demonstrates how although fish is generally a much more important protein source than bushmeat there, the two are readily substitutable, and a decline in fish supply results in an increase in bushmeat hunting (Brashares *et al.* 2004). Recent evidence from Amazonia also demonstrates an increase in bushmeat hunting in response to falling high water season CPUE (Endo, Peres & Haugaasen 2016). Furthermore, the increased chance of a fishing trip yielding no catch at all in the high water season reduces the relative risk of hunting, an activity which is known to have a relatively high failure rate (Endo, Peres & Haugaasen 2016). This mounting evidence of the substitution of fish for bushmeat raises the question of whether an increase in hunting pressure could occur as an indirect result of other major threats to fish stocks, such as widespread dam construction in the Amazon, Congo and Mekong basins (Carolsfeld *et al.* 2003; Winemiller *et al.* 2016).

The observation of a nutrition transition in rural Amazonian, epitomised by the increase in frozen chicken consumption, has led some to conclude that domestic meat is particularly important for modern Amazonian food security (Nardoto *et al.* 2011; van Vliet *et al.* 2015a; de Jesus Silva *et al.* 2016). However, the low frequency of chicken (around twice per month) and beef (around once a month) consumption, along with the lack of significant differences found between their seasonal consumption found in this study suggests that their importance, albeit increasing, has been overestimated. However we acknowledge a likely continued increase in the nutrition transition as more rural people migrate closer to urban areas (Parry *et al.* 2010a), rural-urban connections increase, and rural incomes increase. Many remote Amazonian households are still unable to access and store meaningful quantities of domestic meat, and therefore increase its consumption in the lean high water season, largely as result of a lack of purchasing power, physical accessibility, and refrigeration capacity. In fact, a clear inception point in the trend in chicken consumption can be observed at the limit of Manaus-based ferry boats (Fig. 3.4B) which, as well as buying fish, sell chickens and supply communities with a regular ice supply. Spatial trends shown here suggest that accessibility and refrigeration capacity may dictate domestic meat consumption, and therefore although it is not consumed frequently, those with reliable ice or refrigerators may be able to consume domestic meat at times they most need it, a pattern which may be hidden by our 'snap-shot' sampling. As the first study to show evidence of continuous spatial patterns in domestic meat consumption in Amazonia (Vliet et al. (2015) show a categorical urban-rural gradient), we make a significant contribution to the understanding of nutrition transition dynamics in the region.

3.5.5. Threat multipliers

Our data strongly suggest that a high-water season crash in fish catch rate is the main cause of seasonal food insecurity in the Amazonian floodplain, albeit less-poor households are buffered from this. Our study addressed seasonal resource constraints but we speculate that other causes of reduced fish catch rate could also drive food insecurity, and exacerbate existing vulnerabilities. Exogenous shocks may lead to absolute reductions in fish biomass, for example through more intensive overharvesting (Endo, Peres & Haugaasen 2016), or dam construction (Carolsfeld *et al.* 2003; Winemiller *et al.* 2016). Additionally, as with this seasonal example, exogenous shocks may lead to a reduction in fish availability, such as through climate-driven flood intensification. The four greatest threats to Amazonian freshwater ecosystems are considered to be dam construction, deforestation, pollution, and overfishing (Castello *et al.* 2013). Assuming these threats also reduce fish community catch rate, we infer from the processes observed in this study that food insecurity will likely result.

The Amazonian flood pulse has already increased in amplitude as a result of climate change (Gloor *et al.* 2013; Marengo *et al.* 2013). Flood intensification can further exacerbate existing vulnerabilities in the high water season by increasing the severity and duration of flooding. In terms of food security, the increase in Amazonian flooding is particularly challenging for *ribeirinhos* who suffer from shorter agricultural growing seasons on the floodplain, considerably reducing the biomass of agricultural produce, namely the staple carbohydrate manioc. At the other extreme, the Amazon is also experiencing longer and more intense droughts, which can result in mass fish mortality through hypoxia (Pinho, Marengo & Smith 2015), increased risk of human predation of larger vulnerable megafauna, and an inhibition or prevention of navigability of many rivers. This latter issue may have an increased impact on many of the many roadless communities and towns around the Amazon that rely on the rivers for transportation, including the import of food. Consequently, where food security is already compromised to some extent these changes may cause more serious malnutrition problems in the future.

The increased food insecurity observed in the high water season may be further accentuated due to the high vulnerability of people living in the Amazonian floodplain. A lack of refrigeration capacity and remoteness among much of the population means that domestic meat may not be available when it is most needed. Livestock can act as a safety net during lean seasons or environmental shocks in rural Amazonia (Takasaki, Barham & Coomes 2010; Coomes *et al.* 2010), although the lack or shortage of accessible *terra firme* in many areas dominated by floodplain makes raising livestock a challenging and high risk strategy (Chibnik 1994) due to losses from drowning and pests (Chibnik 1994; Parry 2009; Coomes *et al.* 2010). The lack of reliance on self-raised livestock in this study system is clear as 94 % of the households that had reported chicken consumption had consumed frozen battery-farmed chicken. The food insecurity caused by low fish availability and the lack of alternative meats may be particularly harmful to the health of a vulnerable population with high prevalence of malaria, anaemia and diarrhoea.

3.6. Conclusion

We demonstrate severe seasonal food insecurity among rural inhabitants of the Amazonian floodplain. We present strong evidence that this food insecurity is driven by low fish catch rates during the high water season, which despite increased fishing effort, results in a lower fish catch. Our results are consistent with previous evidence of reduced fish catch rates in the high water season, although to our knowledge this is the first study to provide mechanistic evidence linking reduced wildlife availability to household food insecurity. Seasonal food insecurity may cause significant negative health implications to this population that are so heavily reliant on fish to provide a large proportion of their protein, calories and micronutrients such as iron. The floodplain population is particularly vulnerable even to short periods of inadequate fish supply due to a susceptibility to gastroenterological infections, resulting in dietary nutrient losses and contributing to high rates of iron anaemia, which is particularly dangerous to a population in which malaria is widespread. We show that food security is not equal between households, as more deprived families with larger household population sizes suffer the most, and are therefore most exposed to these health risks.

Our evidence implies that food insecurity is not being exacerbated by commercial overfishing in this part of the Amazon. This respite is probably due to a combination of fishing CPUE hyperstability when overexploited large fish are replaced by smaller fish - and because the mechanisms facilitating overfishing (city-based ferry boats) by purchasing fish and providing ice, also support food security by providing refrigeration (ice) and selling alternative domestic and processed meats. We show that domestic meat consumption is greater nearer urban areas, although it is infrequent and does not change in response to seasonal food insecurity. Consequently, although wild fish constitutes most of their diets and its natural seasonal catch rate variability dictates food insecurity, anthropogenic changes such as climate change that may further reduce fish catch rates could exacerbate current food insecurity.

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3.8. Supplementary information

3.8.1. Supplementary figures

Fig. S3.1. Fishing gear used in the high water and low water seasons. Frequency of fishing trips that utilised different fishing gear, split by season.

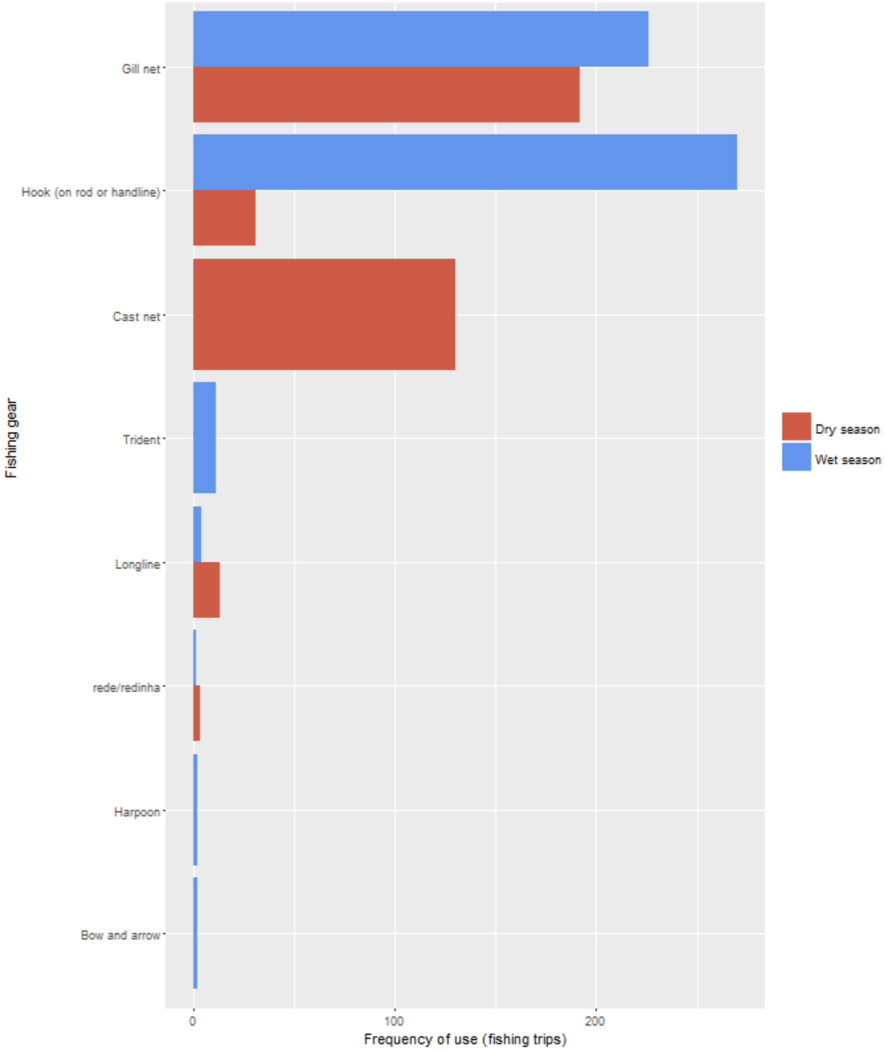


Fig. S3.2. Gill net fishing fish catch rates (CPUEb) per fishing trip, split by season

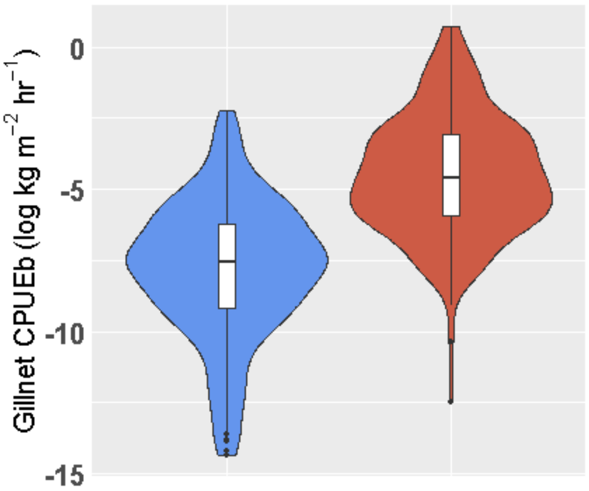


Fig. S3.3. Hook fishing (rods or hand-lines) fish catch rates (CPUEb) per fishing trip, split by season

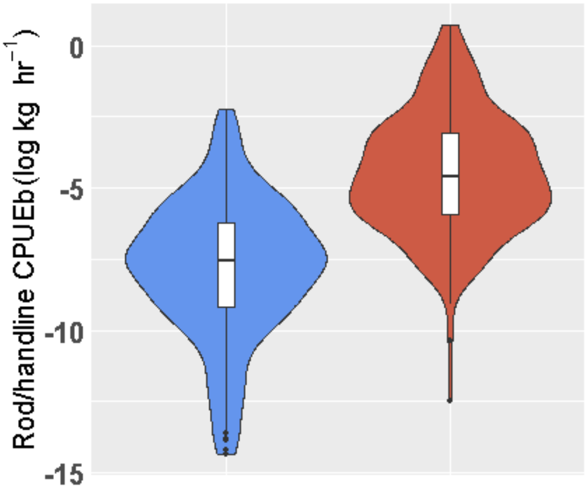


Fig. S3.4. Fishing habitats used in the high water and low water seasons. Frequency of fishing trips that utilised different fishing habitats, split by season

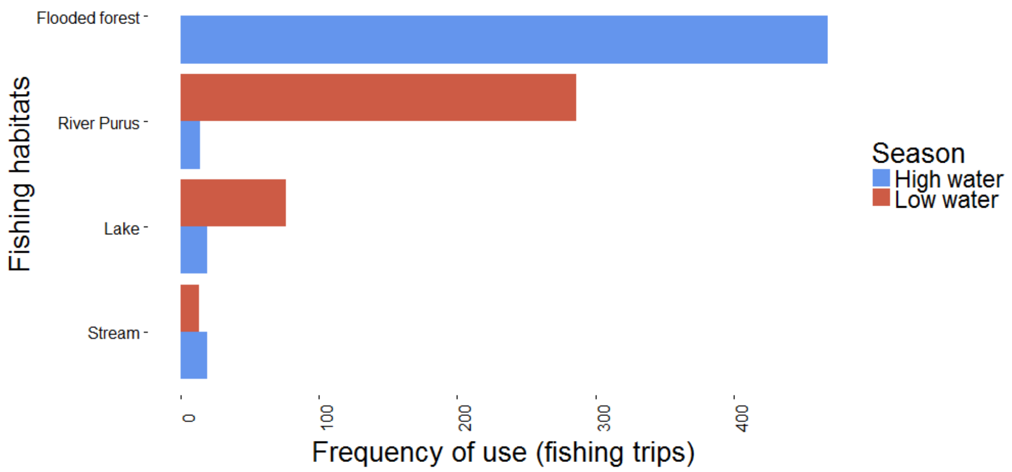
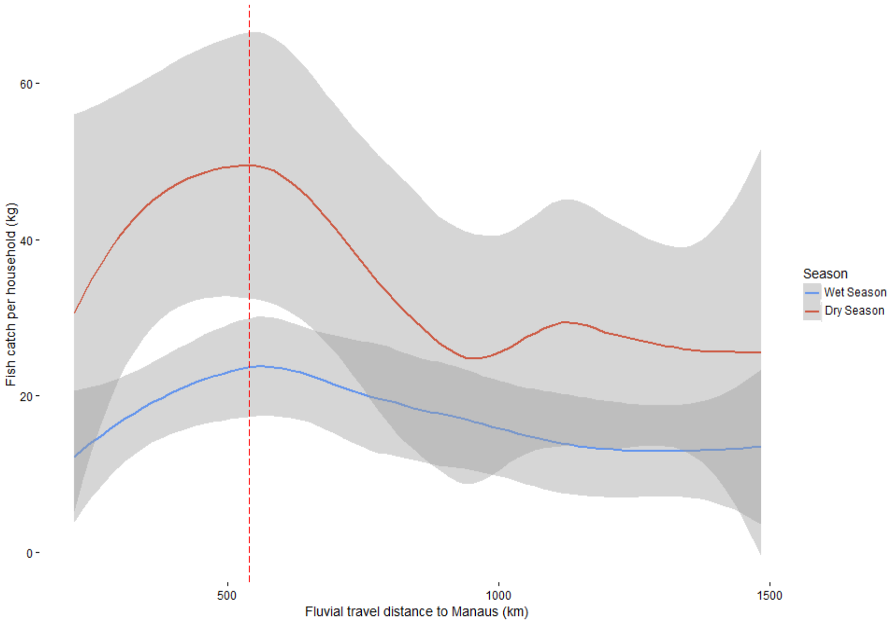


Fig. S3.5. The relationship between the biomass of fish caught (catch) per household and distance to Manaus, split by season. The vertical red dotted line represents the limit of Manaus based *recreio* boats that buy fish, sell domestic meat, and deposit ice.



3.8.2. Supplementary tables

Table S3.1. Bushmeat species body masses. References: 1 = (Dunning Jr. 1992), 2 = (Emmons & Feer 1997)

English name	Scientific name	Local name	Average body weight (kg)	Weight reference
Horned Screamer	*Anhima cornuta*	Alencó	3.15	1
Brazilian Tapir	*Tapirus terrestris*	Anta	238.5	2
Scarlet Macaw	*Arara macao*	Arara vermelha	1.015	1
Heron family	*Ardeidae* family *(Ardea cocoi)*	Manguari, Garça	3.2	1
Collared peccary	*Pecari tajacu*	Catitu	26	2
Capybara	*Hydrochoerus hydrochaeris*	Capivara	50	2
Anhinga	*Anhinga anhinga*	Carará	1.235	1
Black agouti	*Dasyprocta fuliginosa*	Cutia	4.45	2
Purus red howler monkey	*Alouatta puruensis*	Guariba	7.35	2
Tinamou (no i.d.)	*Crypturellus undulatus*	Inambu (no i.d.)	0.567	1
White-throated tinamou	*Tinamus guttatus*	Inambu galinha	0.688	1
Undulated tinamou	*Crypturellus undulatus*	Inambu macucao	0.567	1
Guan (no i.d.)	*Penelope* spp. *(Penelope superciliaris)*	Jacu	0.895	1
Gray woolly monkey	*Lagothrix cana cana*	Macaco barrigudo	6.9	2
Tufted capuchin	*Cebus apella*	Macaco prego	3.1	2
Spider monkey	*Ateles paniscus*	macaco preto	10.5	2
Whistling duck	*Dendrocygna* spp.	Marreca	0.7518	1
Neotropical cormorant	*Phalacrocorax brasilianus*	Mergulhão	1.165	1
Green ibis	*Mesembrinibis cayennensis*		7.56	1
Razor-billed currasow	*Pauxi tuberosa (Mitu tuberosum)*	Mutum de fava	2.813	1
Wattled currasow	*Crax globulosa*	Mutum pirui	2.55	1
Paca	*Cuniculus paca*	Paca	9.5	2
Muscovy duck	*Cairina moschata*	Pato do mato	2.45	1
New World porcupine	*Erethizontidae* family	Quandu	4.25	2

	(Coendou prehensilis)			
White-lipped peccary	*Tayassu pecari*	Queixada	35	2
Armadillo (no i.d.)	Unspecified armadillo (mean on 4 Purus spp.)	Tatu (no i.d.)	11.9625	2
Giant armadillo	*Priodontes maximus*	Tatu açu	30	2
Red brocket deer	*Mazama americana*	Veado vermelho	36	2

Chapter 4

EXPLORING HARVESTER VULNERABILITY THROUGH ANALYSIS OF FISH AND BUSHMEAT CATCH COMPOSITION

Left: a typical Amazonian lake fish catch of tucunaré (*Cichla monoculus*) and aruanã (*Osteoglossum bicirrhosum*), top-right: preparing howler monkey (*Alouatta puruensis*) for the pot, bottom-right: drying salted fish in the sun for preservation. Photo credits: Daniel Tregidgo

Exploring harvester vulnerability through analysis of fish and bushmeat catch composition

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4.1. Abstract

Overharvesting threatens many of the billions of people that rely on wildlife for nutrition and livelihoods; illustrated by estimates that a fifth of the world's population are vulnerable to nutrient deficiencies from falling global marine fish catch alone. Yet identifying human vulnerability through catch composition, which reflects both biological communities and human choice, is rarely considered despite heterogeneous threats to, and values of species. Consideration of the interacting aquatic and terrestrial wildlife harvest profile is even less common, despite some evidence for a substitution of bushmeat for fish. Here we explore how the freshwater and terrestrial species harvested by rural people living in the Amazonian floodplain may indicate their vulnerability to population depletion of key prey species. In high and low water seasons we used harvester interviews to record the fish species and quantities caught by rural fishers during 886 fishing trips. Fishers caught 80 fish species, yet four species made up the majority of harvested biomass. Species reliance varied in time and space, shown by significant variation in fish catch composition between seasons and according to geographical remoteness from the metropolitan centre, Manaus. We consider local people to be most vulnerable during the high water lean season, when overall fish catch rate is low and severe food insecurity is widespread. During this time, we found that local people were highly dependent on the threatened fish species, tambaqui *Colossoma macropomum*, and that they attempt to cope with this seasonal fishing shortfall by

harvesting more bushmeat, particularly a large primate and duck species. We found that in less remote areas, where market connectivity is linked to refrigeration and regular fish-buyer boats, the catch was dominated by species of highest commercial value. In contrast, remote communities with less market integration focussed on catching and salting several species of migratory catfish, with high intrinsic vulnerability to dam construction. Our results provide the first evidence that hunting offtake may increase in response to severe food insecurity, which reinforces calls for coordinated management of bushmeat, fisheries and human well-being.

4.2. Introduction

Billions of people are thought to rely on wildlife harvest (fishing or hunting) for their livelihoods and food security (Milner-Gulland & Bennett 2003; Golden 2016; Lynch *et al.* 2016). Those most reliant on harvesting wildlife are often some of the poorest and most vulnerable people in the world (de Merode, Homewood & Cowlishaw 2003; Brown & Williams 2003; Béné 2009), commonly with few alternative sources of income and nutrition, thus making them highly sensitive to changes in wildlife populations (Golden *et al.* 2011; Golden 2016). Yet, wildlife harvest is a major contributor to pan-tropical defaunation because exploited populations are widely harvested above the maximum sustainable yield (Milner-Gulland & Bennett 2003; Allan *et al.* 2005; Dirzo *et al.* 2014; McCauley *et al.* 2015; Ripple *et al.* 2016). The severe decline in the abundance of exploited species can cascade onto ecosystem functioning and human well-being, threatening livelihoods and causing food insecurity by reducing access to safe and affordable sources of protein, fat and micronutrients (Dirzo *et al.* 2014; McCauley *et al.* 2015).

The paradox that many harvesters are reliant on the same resource to which they are depleting has long been recognised (e.g. Hardin 1968). In particular, humans livelihoods and diets are highly dependent on fish, which provides the global population with around 17% of its animal protein intake; rising to over 50% in many developing countries (FAO 2016). Worryingly, global marine fish catch has been falling by ~1% per year since around 1996 (FAO 2011; Pauly & Zeller 2016), leading to predictions that 19% of the world's population are vulnerable to nutrient deficiencies in the coming decades due to falls in marine catch rates (Golden 2016), if vulnerability is defined as the susceptibility to harm in response to exposure to a threat(s) (Rogers, Castree & Kitchin 2013). Production and consumption data are scarce in bushmeat (Milner-Gulland & Bennett 2003) and freshwater systems (Youn *et al.* 2014; Bartley *et al.* 2015; McIntyre, Reidy Liermann & Revenga 2016), although evidence suggests that dependent human populations across the tropics are vulnerable to increasing terrestrial (Milner-Gulland & Bennett 2003; Golden *et al.* 2011) and freshwater (Youn *et al.* 2014; Lynch *et al.* 2016) defaunation. Populations reliant on freshwater fisheries may be particularly vulnerable, because defaunation has been more severe in freshwaters than marine and terrestrial realms (Dudgeon *et al.* 2006; Young *et al.* 2016). Moreover those dependent on freshwater fish are almost exclusively poor, with 95% of catch coming from developing countries (Bartley *et al.* 2015).

Despite the importance of defaunation for livelihood and food security our understanding of people's vulnerability may be undermined by an over-reliance on harvested biomass data, which may mask many important impacts of species compositional changes on human vulnerability. Inferences about human vulnerability from catch data can be complicated by a number of factors including changes in harvester behaviour, and differences in the importance of certain taxa to nutrition and livelihoods. Catch biomass in an overfished fishery can initially remain high as fishers increase effort and diversify the species exploited (Pauly *et al.* 1998; Allan *et al.* 2005). For example, the world's oceans have been unsustainably exploited for centuries (Roberts 2007) and CPUE (catch-per-unit-effort) has been falling for decades (Watson *et al.* 2013), yet global marine fisheries catch only began to decline twenty years ago (FAO 2011; Pauly & Zeller 2016). As such, we cannot assume that defaunation will result in catch declines and resultant harm to wildlife-reliant populations (Chapter 3).

While harvesters may manage to maintain the biomass caught in an overharvested system, livelihoods are also dependent on species catch composition and associated market prices (Lam *et al.* 2016). For example, where bushmeat markets are strong, larger terrestrial species are often sold to urban bushmeat consumers, while smaller less-profitable species are more likely to be consumed within hunter camps or rural households (van Vliet & Nasi 2008; Kümpel *et al.* 2010; van Vliet, Nebesse & Nasi 2015). The decline in abundance of larger species and shift to smaller-bodied species frequently results from overharvesting (Allan *et al.* 2005; Dirzo *et al.* 2014; McCauley *et al.* 2015; Ripple *et al.* 2016). This is largely due to a general preference among harvesters (Bodmer 1995) and consumers (Allan *et al.* 2005; Kümpel *et al.* 2010) for large-bodied wildlife. For example, the mean maximum total length of fished species in the Amazon reduced from ~206 cm in 1895 to ~76 cm in 2007 (Castello *et al.* 2013).

There may be complex spatio-temporal variation in the linkages between overharvesting and both livelihoods and food security, as human reliance on different species varies in both space and time. For example, access to markets and refrigeration capacity can transform the catch of harvesters by increasing the catch biomass, particularly of commercially important species (Mcgrath *et al.* 1993; Brewer *et al.* 2012). Some taxa only form a significant part of harvester catch during seasonal migrations when availability is high (Mcgrath *et al.* 1993; Nyahongo *et al.* 2009). Other wild meats only become important when the accessibility of alternative meats becomes restricted, thereby acting as important nutritional safety nets. For example, bushmeat harvest and consumption may significantly increase during periods of low agricultural output (de Merode, Homewood & Cowlishaw 2004) or lower fish catch rates (Poulsen *et al.* 2009; Endo, Peres & Haugaasen 2016). Reliance on different taxa is therefore spatially and temporally variable among wildlife harvesters, yet researchers have rarely considered this when investigating livelihoods and food security.

Irrespective of wildlife population declines, the vulnerability of human harvester populations also varies in time and space. The most common form of food insecurity is that suffered seasonally (Vaitla, Devereux & Swan 2009; Barrett 2010), and lean seasons are common in both agricultural and harvester systems (Ferro-luzzi *et al.* 2001). Remote populations may be particularly vulnerable to food and livelihood insecurity (Maru *et al.* 2014), as they have limited access to urban markets to buy and sell food and other goods. Although the vulnerability of harvesters and their dependence on different wildlife taxa vary in time and space, taxonomic specificities are rarely factored into the assessment of human vulnerability to wildlife declines (Lam *et al.* 2016). Our focus here is principally on rural people, as urban people have more access to alternative foods such as domestic meat, and are also less dependent on these harvests for income.

Very few studies assess both offtake from terrestrial sources and catch from fisheries, which may mask compensatory behaviour. While the labels ‘fisher’ and hunter’ are often used in harvesting studies, both fish and bushmeat commonly make up important components of the catch profiles of a ‘harvester’ in tropical forested areas. Hence, studies that focus only on either fishing or hunting alone may be missing potential interactions between aquatic or terrestrial harvest, and there is limited but growing evidence for harvester compensatory behaviour in tropical forest settings. Difficulties in catching fish due to overfishing-driven abundance declines (Brashares *et al.* 2004) or seasonal CPUE declines (Endo, Peres & Haugaasen 2016) have been blamed for increased hunting activity. However, these studies focus on relative fish and bushmeat biomass, and not on species. A species focus is important when we consider that demand, intrinsic vulnerability, and threats are species-specific, and that management often acts on particular species (e.g. Amazonian fish minimum size restrictions). Nevertheless, these studies demonstrate the importance of considering terrestrial and aquatic wildlife in tropical harvester studies concerned with biodiversity conservation and/or human well-being.

4.2.1. Study aims

Research into the impacts of wildlife declines on livelihoods and food security tends to consider only the effects of variation in harvested biomass. Hence, the importance of spatial and temporal variation in catch composition is commonly overlooked. This is particularly important when we consider that access to food and markets often varies in space and time, and that the nutritional and economic value of wildlife differs between species.

We address these knowledge gaps by exploring variation in fishing and bushmeat catch composition of rural harvesters in the Amazonian floodplain. We consider this rural population to be vulnerable during the high water season when they experience severe food insecurity (Chapter 3), and in remote areas with poor urban connections (Chapter 2). Firstly, we ask how do spatial, temporal and landscape factors determine fish and bushmeat catch composition in this harvesting system? Secondly, which taxa contribute most to dissimilarities observed in time and space? Finally, are there changes in the biomass of bushmeat hunted per household which can be associated with fish catch rates? We hypothesise that catch composition will vary significantly between season, with distance from urban markets and within different landscapes, and that hunting will increase when and/or where fishing catch rates are low. These research questions are explored using data concerning the fishing and hunting catch rates and species catch composition of rural harvesters, collected over a gradient of travel distance to the city of Manaus, during the peaks of the high and low water seasons.

4.3. Methods

4.3.1. Study area

The study was carried out in rural communities in the floodplain along the mid-lower River Purus in the Brazilian Amazon. The River Purus supplies more fish to the Amazon's largest city, Manaus (population 2.1 million people; IBGE, 2010), than any other river (Batista & Petrere Júnior 2003; Cardoso *et al.* 2004; Gandra 2010). Demand from Manaus has been attributed to causing overfishing of the commercially important tambaqui (*Colossoma macropomum*) in the river (Chapter 2). However, apart from overfishing, the mid-lower Purus does not suffer significantly from the other major threats of Amazonian freshwater degradation: deforestation, pollution and dam construction (Castello *et al.* 2013). The mid-lower Purus River catchment meets the definition of a wilderness area (Mittermeier *et al.* 1998), with high remaining forest cover, and low human population densities (Table 1.2). It is the only major Amazonian tributary whose watershed remains undammed, and one of three with an undammed main channel (Winemiller *et al.* 2016).

The River Purus sees some of the highest seasonal amplitudes (~15 meters) in river levels in the Amazon Basin (Castello & Macedo 2016), transforming much of the catchment into flooded forest. The seasonal flood pulse has an enormous impact on aquatic and terrestrial ecology and the activities of the local people in the Amazonian floodplain (Junk, Bayley & Sparks 1989; Endo, Peres & Haugaasen 2016). Data were collected during high water (April – July 2014) and a low water (August – November 2014) field seasons. This also avoided working during the *defeso* fishing closed season (de Almeida Corrêa, Kahn & Freitas 2014), thereby avoiding another level of variation in fishing activity or the reporting of. The timing of our two descents of the River Purus were intended to accompany the fluctuating water levels, aiming to visit each sampled community at approximately the peak and trough of annual water levels. In order to achieve this, we planned the timing of the journeys on the river-level calendar based on long-term averages (Coe *et al.* 2002).

4.3.2. Sampling

Our sampling was designed to enable us to test for spatial, temporal and landscape differences in harvesting, in relation to remoteness from Manaus, the seasons, and local extent of *terra firme* and *várzea* flooded forest cover. We worked downstream of the town of Lábrea and upstream from the confluence with the River Solimões, visiting 22 communities. From the first to the last community the fluvial travel distance along the River Purus was 1267 km, as calculated using the travel network function in ArcGIS 10.2.2 (ESRI 2014). Travelling downstream, our protocol was to stop at the first community we came to that (a) had 10-30 residences, (b) had fishing and hunting grounds relatively independent of other sampled communities (mean = 61 km travel distance between communities, minimum = 13 km), and (c) avoiding communities around the federally-designated Abufari Biological Reserve. Regulation and monitoring concerning harvesting practices were much more intense in and around the Abufari Biological Reserve than in sustainable use reserves or unprotected areas, potentially affecting wildlife populations and harvester-responses to interviews. The percentage flooded forest within a 5 km radius of the community ranged between 16.3-92.2% (mean 59.0%), but there was no significant trend with distance to Manaus (P = 0.5).

An unexpected challenge of sampling was encountered in several communities that were partially or fully abandoned at high water, which for some people was an ordinary annual routine (many people go to houses on the *terra firme* '*por centro*' deeper in the forest during ordinary floods (Winklerprins 1992)), or because other people had abandoned their flooded houses as 2014 brought exceptionally high waters (Espinoza *et al.* 2014). Communities entirely abandoned at the time of encounter at high water were visited neither at high nor low water.

We visited a maximum of 20 households per community (mean = 13.2 per community visit). Where a community had more than 20 households, we would ask the village president (or another representative where absent) for the name of the head of each household, which they would then select randomly in a lottery system. Within each household we interviewed every resident of 16 years of age or older that had been fishing or hunting in the past 30 days. Interviews were used to collect data concerning fishing and hunting activities.

4.3.3. Fishing and hunting data

Conservation scientists are increasingly utilising interviews with resource-users to draw on local ecological knowledge in order to obtain relative or absolute estimates of harvest levels and species abundance, for example Coad *et al.* (2013). Collecting data on harvester catch and effort has been shown to be cheaper and more efficient than ecological methods, yet with similar levels of accuracy and precision (Thurstan *et al.* 2015).

All surveyed fishers were asked in detail about the species catch composition, effort applied and catch methods of every fishing trip (whether successful or not) that they had undertaken in the 72 hours prior to the interview. To keep response variables spatially associated with the community's location, we restricted information to harvesting trips that had occurred within 2 hours journey by motorised canoe (*rabeta*) from the harvester's home in the community. Insights from a pilot study indicated that two hours of travel time was a measure to which local people could accurately relate, equating to a standard distance of around 18 km fluvial travel distance from the community (Parry & Peres 2015). Regarding catch, respondents were asked to identify every animal caught (to species level where possible), and approximately how many individuals of that taxa that had been caught.

Of the 80 fish types reported, four were not identified to species level. These three fish types were known locally as cará açu, consisting of *Astronotus crassipinnis* and *Astronotus ocellatus*, piranha branca consisting of *Pristobrycon striolatus* and *Serrasalmus gouldingi*, bodó consisting of the *Liposarcus* genus; mainly *Liposarcus pardalis* (Santos, Ferreira & Zuanon 2006), and sarapó, which are Gymnotiformes (Table S4.1). They were grouped together because many local people were often unable to distinguish between them.

In tables and figures we collectively refer to “other birds” in reference to various species of heron (Ardeidae family), scarlet macaws (*Arara macao*), guans (*Penelope* spp.), tinamous (Tinamidae; mainly *Crypturellus undulates* and *Tinamus guttatus*), whistling ducks (*Dendrocygna* spp.), horned screamers (*Anhima cornuta*), anhingas (*Anhinga anhinga*), neotropical cormorants (*Phalacrocorax brasilianus*), and green ibis (*Mesembrinibis cayennensis*).

As with fishing surveys, we also used detailed hunting surveys to collect data on harvesting activity during the previous 72 hours. However, there were too few hunting events reported in this time period to use this data in this study. We therefore used hunting recall data from the 30 days prior to interview, which only included the species (or broader taxon where unidentifiable) and quantity hunted. These catch data were converted into biomass using additional standard species weights, which we generated from primary and secondary data for fish (Table S4.1) and secondary published data for bushmeat (Table S3.1).

Our pilot study confirmed previous work (Pinho, Orlove & Lubell 2012) that states that where fish are sold directly by the fisher per unit weight, the fisher can estimate biomass of these species accurately. In our study system this was the case for larger species (those that commonly weighed >1kg), namely the large catfish (*Pseudoplatystoma fasciatum*, *Phractocephalus hemioliopterus*, *Pseudoplatystoma tigrinum*, *Brachyplatystoma filamentosum* and *Zungaro zungaro*), *Arapaima gigas*, *Colossoma macropomum*, *Osteoglossum bicirrhosum* and *Piaractus brachypomus*), which were commonly sold species, and priced per kilogram. In the few cases that these estimates were missing (rarely, fishers felt unable to estimate) a mean of all other estimates of the relevant species weight was used. Smaller species were however commonly fished for subsistence or sold per individual, and fishers found estimating biomass of these species more challenging during the pilot study, so we therefore did not rely on fisher biomass estimates for these species, and instead calculated catches using standard species weights.

While maximum species weights can be derived from FishBase (Froese & Pauly 2015), we wanted to accurately represent landed species weights. This was challenging to obtain in the field because we required the average weight that was caught and landed by a local fisher as uninfluenced by the researcher, and hence we were unable to weigh (a) fish caught by ourselves, or (b) fish that we asked a fisher to catch for us. We therefore opportunistically weighed 1515 fish individuals of 78 species (plus 2 genera, not identified to species level) that were caught and landed by local fishers, uninfluenced by the researcher. A mean weight per species was used in analyses for those weighed, however where weights lacked for certain rarer species, we calculated mean landed weight. We calculated the maximum species weight by inputting maximum lengths and relevant coefficients from FishBase (Froese & Pauly 2015) into the fish weight-length equation. We then calculated how much smaller the fish landed by Purus fishers were than maximum sized fish from the literature (Santos, Ferreira & Zuanon 2006; Froese & Pauly 2015), finding that the mean landed fish was 60-89% (reduction factor) of the maximum species weight. Reducing the maximum species weight by the calculated reduction factor of the closest related species possible where FishBase data was available, gave us our estimates of mean landed weights for each species. The overall weight of fish caught in each harvesting trip (past 72 hours) was calculated by multiplying the number of individuals caught of a particular fish species by the standard tabulated mass for that species.

4.3.4. Statistical Analysis

Distance based linear models (DistLM) were used to model the relationship between a multivariate species resemblance matrix (describing similarities between species presence, abundances or biomass) and several environmental predictor variables. DistLM is used in studies that look to explain species compositional differences within ecological communities (e.g. Moore, Harvey & Van Niel 2010). In essence, DistLM tells us which environmental variables best explain the (dis)similarities in species presence, biomass or abundance, and how much variation they explain. Resemblance matrices were made for (1) the presence/absence and (2) the biomass of the 20 fish species with the greatest total biomass that were caught in the 72 hours prior to interview. Resemblance matrices were also made for (3) the presence/absence and (4) the abundance of the 12 bushmeat taxonomic groups hunted in the 30 days prior to interview. For analyses of biomass and abundance data, the Bray-Curtis similarity index was used, whereas the Sorensen similarity index was used for presence/absence data. All data were aggregated to the level of community by season (n = 43, as 22 communities were visited during the high and low water seasons, apart from one that was abandoned in the low water season). The environmental predictor variables were season, distance to Manaus, distance to the nearest town, human population density, and percentage *várzea* flooded forest, plus percentage *terra firme* for bushmeat. We used the forward selection of models, and adjusted-R^2.

We used similarity percentage (SIMPER) analyses to identify the fish species that most contributed to the dissimilarity in fish assemblages (e.g. Hallwass & Silvano 2016) between variables in the significant models. The software Primer+Permanova (Clarke & Gorley 2006) was used to perform DistLM and SIMPER analyses. SIMPER analyses compare two categories, which we used as seasons (high and low water), flooded forest cover (< or > 50%), and distance to Manaus (communities near Manus that receive regular visits from urban boats that deposit ice and sell fish, and remote communities that do not). The latter (fish preservation method) was a useful way to group geographic remoteness, and although communities receiving ice regularly were only those closer to Manaus, it was distinct to the continuous kilometre scaling used in the DistLM tests.

Hunted bushmeat biomass per household was modelled using R statistical software version 3.1.3 (R Core Team 2015). Due to the high number of households with zero hunting offtake, we used a zero-inflated GLMM (general linear mixed-effect model) with community as a random factor to test for trends in the *glmmADMB* package. Model diagnostic plots were subsequently inspected. A P-value was calculated using likelihood ratio tests.

4.3.5. Ethics

Our research proposal was assessed and approved by ethics councils in both Lancaster University (United Kingdom) and the Federal University of Lavras (Brazil). Article 37 of Brazilian law 9605 from 1998 states that killing an animal is not a crime when it is carried out to satisfy the hunger of the harvester or their family. As we intentionally do not specify which fishing and hunting activity was commercial, we do not associate any person or community with illegal activities in order to maintain anonymity.

4.4. Results

We recorded the recent catch of 385 different fishers from 886 fishing trips, during the high and low water seasons in 2014. The mean biomass of fish caught per household in the 72 hours prior to interview in the high water season (16.9 kg) was approximately half of that in the low water season (32.1 kg) (Chapter 3; Fig. 4.1B). We recorded 25,787 individuals of 80 species of fish. Despite this high species richness caught, a fraction of these species made up the vast majority of the total biomass of fish landed (Fig. 4.2). For example, over half of the biomass caught came from just four species; the common pacu *Mylossoma duriventre*, the silver arowana *Osteoglossum bicirrhosum*, the tambaqui and the arapaima *Arapaima gigas* which is the biggest scaled freshwater fish species in the world. Thus we only analysed variation in the catch composition of the twenty most important fish species by biomass (Fig. 4.3), which we deemed sufficient to capture seasonal and intra-community variation. We asked about the bushmeat hunting activity during every of the 270 and 296 household visits made in the respective high and low water seasons. A total of 82 households reported to catching anything in the 30 days prior to interview.

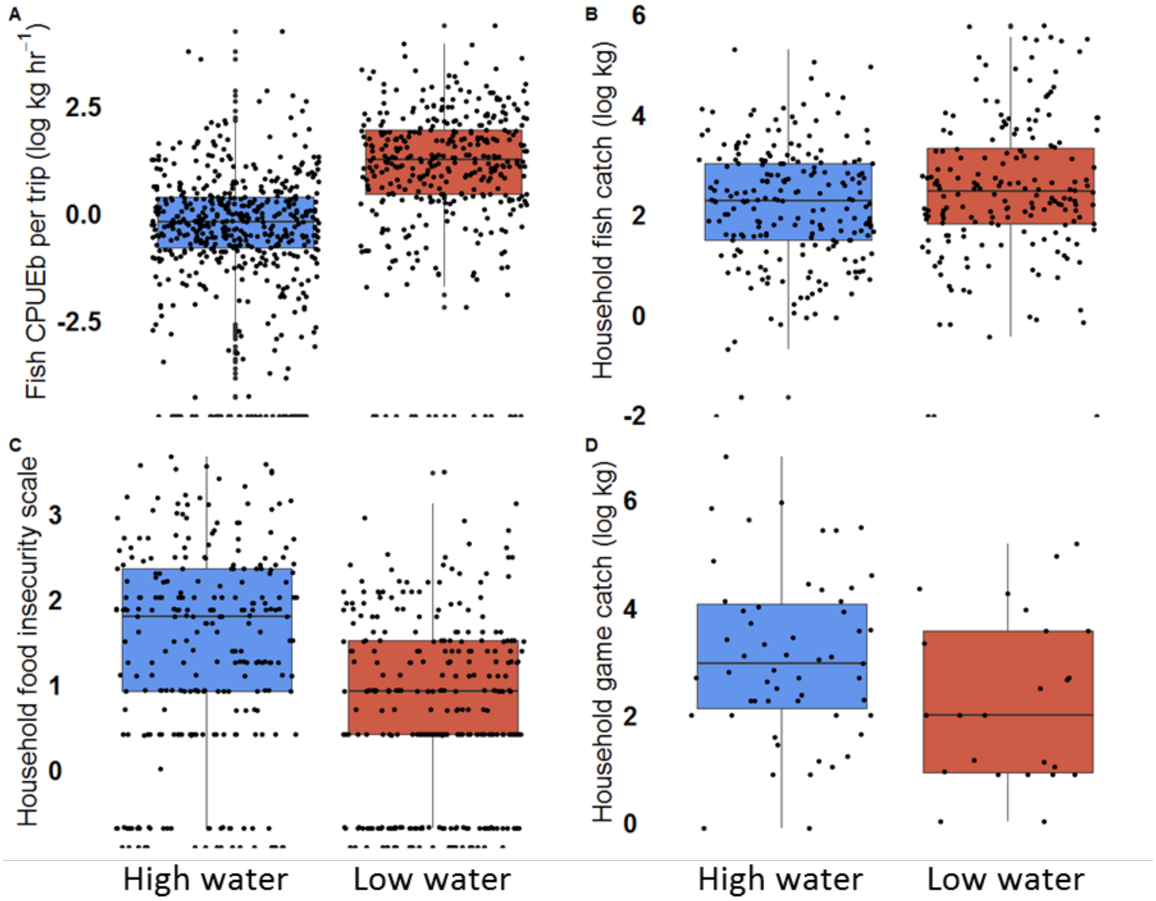

Fig. 4.1. Seasonal variation in (A) fish CPUE, (B) fish catch biomass, (C) food insecurity, and (D) bushmeat catch biomass. We suggest causation by proposing that seasonally high waters result in reduced fish CPUE, hence reduced fish catch per household, explaining greater food insecurity, which harvesters react to by increasing the biomass of bushmeat caught per household. Fish catch is the total caught in the 72 hours prior to interview, while hunted catch is from the prior 30 days. Figures A-C are also presented in Chapter 3, and are shown here to aid comparison with panel D.

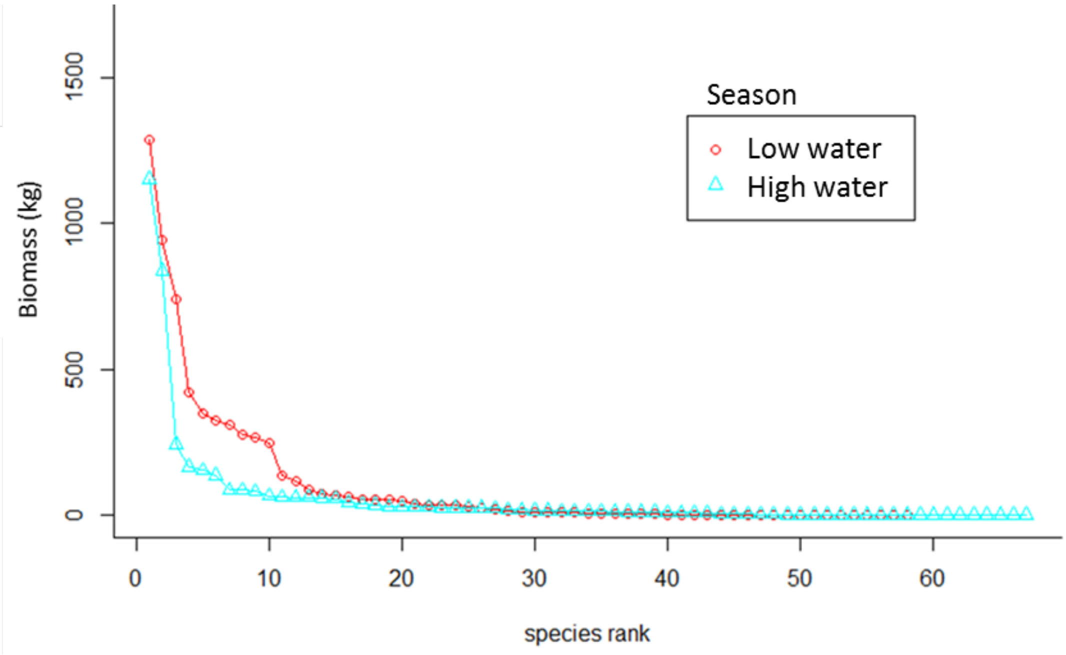

Fig. 4.2. Fish species rank curve (by biomass), showing the domination of a few species in the catch, particularly in the high water season (blue triangles). We use this to justify restricting statistical analyses to the 20 most species of greatest cumulative biomass.

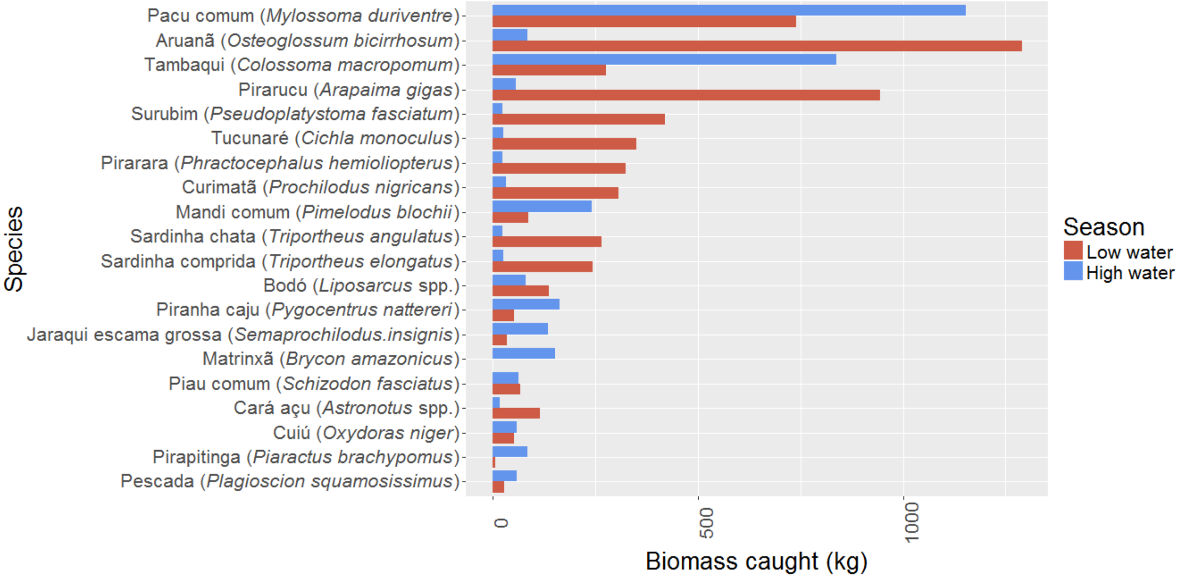

Fig. 4.3. The most important 20 fish species by total biomass caught, in descending order, split by season.

4.4.1. How do geographic remoteness, seasons, and place-based (landscape) factors determine dissimilarities in fish and bushmeat catch composition?

DistLM analyses support our prediction that distance from Manaus and season explain much of the difference in fish catch composition (Table S4.2 and S4.5). Both were highly significant ($P < 0.001$) and together explained 30% of total variation in catch composition (Table S4.3), responsible for the observed fish species presence/absence.

Table 4.1. DistLM significant model results showing factors explaining dissimilarities in fish catch composition. Adj. R^2 refers to adjusted R^2 values, and F refers to pseudo-F values. See Tables S4.4 and S4.5 for DistLM marginal test results.

	Biomass data			**Presence-absence data**		
Variables	**Adj. R^2**	**F**	**P**	**Adj. R^2**	**F**	**P**
Season	0.09	4.96	<0.001	-	-	-
Distance to Manaus	-	-	-	0.15	8.20	<0.001
Season + Distance to Manaus	0.16	4.48	<0.001	0.30	9.72	<0.001

Highly distinct differences in seasonal catch composition can be seen visually through NMDS (Non-metric Multidimensional Scaling) graphs (Figs. S1 and S2). High water catch was dominated by the common pacu and tambaqui. Along with the Bloch's catfish *Pimelodus blochii*, which was also mainly caught in the high water (Fig. 4.3), these three species were identified by SIMPER analysis to contribute the most to seasonal dissimilarity in catch composition, together contributing to 35% of this variation (Table S4.4). Catch in the low water season was more diverse, and the silver arowana, the arapaima*,* and the common pacu made up the greatest biomass of fish caught (Fig. 4.2). However, SIMPER analyses show that the dusky narrow hatchetfish *Triportheus angulatus*, the silver arowana, the sorubim catfish *Pseudoplatystoma fasciatum* and the arapaima, which each contribute 5-6% to seasonal catch dissimilarity, contribute most to seasonal differences in favour of the low water (Table S4.4).

Table 4.2. Fish catch composition SIMPER analyses. Fish species that contribute most to the temporal and spatial dissimilarities in catch. Spatially this refers to communities nearer Manaus that have a regular supply of ice, and those further communities that do not, instead relying largely on salting for fish preservation. Refer to Tables S4.6 and S4.7 for full results.

	Season		**Fish preservation**	
Species	**Greater contribution**	**Percentage contribution**	**Greater contribution**	**Percentage contribution**
Mylossoma duriventre	High water	14.64	Ice	19.17
Pimelodus blochii	High water	10.54	Salt	7.48
Colossoma macropomum	High water	10.05	Ice	11.08
Triportheus angulatus	Low water	7.42	Salt	4.86
Osteoglossum bicirrhosum	Low water	6.87	Salt	9.18
Pseudoplatystoma fasciatum	Low water	6.85	Salt	6.50
Arapaima gigas	Low water	6.45	Ice	8.58

Spatially, we compared catch composition differences in those communities nearer Manaus that receive a regular (at least weekly) visit from boats that deposit ice and buy fish, and those further from Manaus that do not. Two commercially important species (Santos, Ferreira & Zuanon 2006), the common pacu and tambaqui, were mainly caught nearer Manaus, making up 30% of the spatial variation in catch composition (Table S4.5). Species with established trade in salted fish, the silver arowana, the sorubim catfish and the redtail catfish (*Phractocephalus hemioliopterus*), were mainly caught in communities further from Manaus, together contributing 20% of the spatial catch composition variation.

DistLM analyses of bushmeat catch showed season to be significant in explaining both the abundance and presence/absence of different bushmeat taxa (Tables S4.8 and S4.9). Presence/absence was also explained by the local flooded forest cover. Bushmeat catch data analyses had much less explanatory power than the fish data analyses, with season explaining just 5% of the variation in terms of presence/absence (Table S4.7) or abundance (Table S4.6), and percentage flooded forest cover explaining 5% for presence/absence data.

SIMPER analyses revealed that Muscovy ducks (*Cairina moschata*) and howler monkeys (*Alouatta puruensis*) were particularly important bushmeat species in areas with high flooded forest cover (>50% within a 5 km radius of the community), contributing 33% of the variation. Most taxa were hunted more in communities with majority surrounding flooded forest cover. The only species that were hunted more in low flooded forest areas were the collared peccary (*Pecari tajacu*) and red brocket deer (*Mazama americana*).

Table 4.3. DistLM significant model results for bushmeat data. Adj. R^2 refers to adjusted R^2 values, and F refers to pseudo-F values. See Tables S4.8 and S4.9 for DistLM marginal test results.

	Abundance data			**Presence-absence data**		
Variables	**Adj. R^2**	**F**	**P**	**Adj. R^2**	**F**	**P**
Season	0.05	2.98	0.017	0.05	2.70	0.018
Season + flooded-forest cover	0.10	2.49	0.045	-	-	-

Table 4.4. Bushmeat catch composition SIMPER analyses. Taxa that contribute most to the dissimilarities between seasons and levels of flooded forest cover**.** High and low refer to those communities with >50% or <50% *várzea* flooded forest cover within a 5 km radius respectively. Refer to Table S4.10 and S4.11 for full results.

	Season		**Flooded forest cover**	
Taxon	**Greater contribution**	**Percentage contribution**	**Greater contribution**	**Percentage contribution**
Howler monkey	High water	16.62	High	16.36
Muscovy duck	High water	16.40	High	16.78
Other birds	Low water	15.07	High	14.49
White-lipped peccary	Low water	12.00	High	12.07
Curassow	Low water	9.79	High	9.16
Paca	High water	9.67	High	8.79
Other primates	High water	6.68	High	5.79
Collared peccary	High water	4.76	Low	5.98

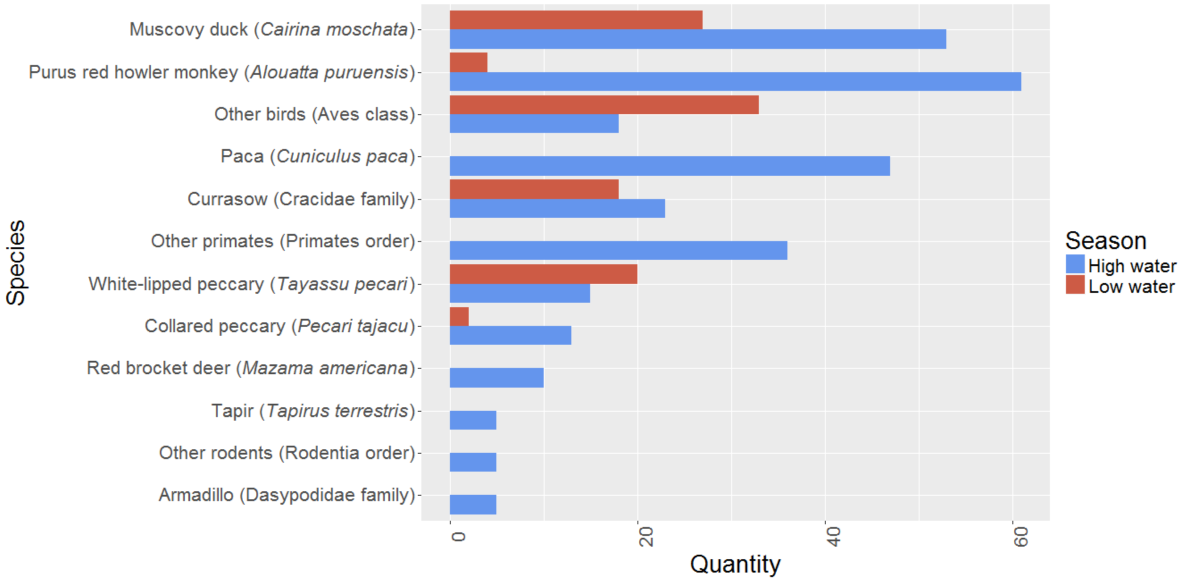

Fig. 4.4. All bushmeat taxonomic groups by abundance hunted, in descending order split by season.

4.4.2. Are there changes in the household bushmeat biomass and catch profile which can be associated with fish catch rates?

The total reported bushmeat catch was approximately four times greater in the high water (3,905 kg; 291 individuals harvested) than the low water season (953 kg; 104 individuals harvested). Mean bushmeat biomass harvested per household was over four times greater in the high water season (14.5 kg per 30 days) than the low water season (3.2 kg), a difference which is highly significant ($P < 0.001$, $n = 566$, Fig. 4.1D). Howler monkeys and Muscovy ducks were the most common species hunted during the high water season (Fig. 4.4). They also contributed the most to the variation observed between seasons according to the SIMPER analyses (Table S4.10), cumulatively contributing 33%. Low water season hunting catch was heavily dominated by birds, namely Muscovy ducks and curassows (*Pauxi tuberosa* and *Crax globulosa*).

4.5. Discussion

This work demonstrates how catch composition varies spatially and temporally in both fisheries and bushmeat in the Amazonian floodplain. It makes important connections between the spatial and temporal vulnerability of wildlife harvesters and the species of fish and terrestrial bushmeat species they harvest. We found evidence of significant alterations in both bushmeat and fish species profiles between seasons, and an overall increase in bushmeat offtake during the high-water season. This is an important finding because this season is also characterised by reduced fish catch rates and high levels of rural food insecurity, particularly among deprived households (Chapter 3; Fig. 4.1 A-C). It is significant that seasonal catch differences were observed for the harvest of both fish and terrestrial bushmeat species, reinforcing linkages between aquatic and terrestrial harvesting systems (Brashares *et al.* 2004; Endo, Peres & Haugaasen 2016). Moreover, our findings support recent work that highlights the important seasonal variation in harvesting in flood pulse systems, the consideration of which could increase the reliability and accuracy of assessments of sustainability and harvester dynamics (Endo, Peres & Haugaasen 2016; Isaac *et al.* 2016).

Our results also show that metropolitan market demand and associated infrastructure appear to play central roles in dictating fish catch composition. This advances current understanding of the spatial dynamics of urban-driven commercial harvesting, which is known to drive increased catch biomass and species defaunation in some tropical systems (Chapter 2; Cinner et al. 2016; Brewer et al. 2009; Parry & Peres 2015).

4.5.1. Seasonal variation

The strong observed seasonal differences in catch composition may be particularly important as harvesters suffer from severe food insecurity in the high water season as a result of significantly lower fish catch rates (Chapter 3; Fig. 4.2 A-C). Some seasonal differences in fish catch composition in Amazonia are expected due to the impacts of the seasonal flood pulse on fish catch rates (Endo et al. 2016; Chapter 3), and the seasonal migratory behaviour of many of the region's fishes (Araújo-Lima & Ruffino 2003). However, reliance on certain taxa may also be high due to differences in both the relative commercial and nutritional value of certain species in the high water lean season. Could a management focus on the sustainable use of the species which harvesters most rely during this time help reduce the vulnerability of local people? This question can be assessed by focussing on the three frugivorous fish species that contributed most to the variation in seasonal catch and were caught more during the high water; the common pacu, the Bloch's catfish and the tambaqui. Evidence that the fishery of one of these species, tambaqui, is collapsing as a result of urban market-driven harvesting pressure (Chapter 2), is therefore worrying. This is a major concern because harvesting this species is particularly lucrative for local people during this period of overall high vulnerability to income-poverty and food insecurity (Fig. S4.3).

While most fishing is undertaken in rivers and lakes during low water, almost all fishing during the high water season occurs in the flooded forest (Fig S3). During this period fruits from floodplain forests dominate the diets of many Amazonian frugivorous fish (Lucas 2008). Local ecological knowledge of this is used to target frugivorous fish under fruit trees, using fruits as bait, and/or through acoustic imitation of fruit falling into the water via a *gaponga* or flicking the water's surface (personal observation; Goulding 1981). For example, the Bloch's catfish was very important in remote communities during the high waters, and local people regularly blamed poor or failed catches on an inability to find sufficient fruit bait (personal communication with Purus fishers). In consuming large quantities of fruit, frugivorous fish accumulate larger stores of fat in high water periods (Junk 1985). Frugivorous fish may be relatively important as a fat source given that some Amazonian fish species have significantly lower fat content during the high water period (Petenuci *et al.* 2016). Due to the severe food insecurity identified in floodplain populations during the high water season, and that fat is generally in more scarce supply than protein in tropical forest-dwellers (Sirén & Machoa 2008), frugivorous fish may play a particularly important role in nutrition during the lean season. This notion is supported by evidence that harvesters in Kenya may have avoided highly available lean terrestrial meat during the lean season in favour of seasonally fatty catfish (Speth *et al.* 1991; Archer *et al.* 2014).

4.5.2. Fish-bushmeat link

The seasonal differences in hunted wildlife catch composition we report also advances current understanding of the fish-bushmeat link. We demonstrate that bushmeat catch is greater, more diverse, and particularly focussed on several important species during the high water season. Mean bushmeat biomass caught per household was four times higher in the lean fishing (high water) season. Hence our correlative evidence that the importance of bushmeat is greater when fish availability is restricted suggests a causative link, although we lack further corroborating evidence that this is the case. There is international evidence that harvesters (Brashares *et al.* 2004; Endo, Peres & Haugaasen 2016) and/or consumers (Apaza *et al.* 2002; Wilkie *et al.* 2005) readily substitute fish for bushmeat. This switch in harvesting practice has been shown to occur when fishing becomes difficult, as a result of overfishing (Brashares *et al.* 2004) or seasonal flooding (Endo, Peres & Haugaasen 2016). There is evidence that fish and bushmeat are dietary substitutes, with relative consumption levels being dictated by seasons (Poulsen *et al.* 2009) and prices (Apaza *et al.* 2002; Brashares *et al.* 2004; Wilkie *et al.* 2005). However, given that our measurements come from the same locations that exhibit severe seasonal food security during the high water season (Chapter 3), this is the first study to link such a substitution to food security measurements. This suggest that harvesters may be making this fish-bushmeat switch due to nutritional vulnerability. As such, despite the flooded forest being rich in wild protein, it may also be the reason why harvesters need to hunt during high waters.

4.5.3. The seasonally flooded forest

Seasonal hunting catch composition analysis shows that a duck and a large primate species appear to become the major targets of hunting pressure during the scarce fishing season, when harvesters switch from fish to bushmeat. Moreover, our results show that the harvest of this duck and primate species is greater where flooded forest cover is high. Presumably howler monkeys and Muscovy ducks were more important during high waters and in areas of greater flooded forest cover because of a tendency of local people to hunt from their canoes in the flooded forest, due to ease of access and carcass transportation. Additionally, the fact that most bushmeat species were mainly hunted in the flooded forest hints at a higher diversity of bushmeat profile in the flooded forest due to an absence of the main *terra firme* species. This study therefore also demonstrates the importance of flooded forest preservation for providing a lean season safety net habitat, as both the main fishing ground (Fig. S3.4), and a determinant of key bushmeat species (howler monkey and Muscovy duck) extraction.

4.5.4. Spatial variation: Ice and salting

As hypothesised, commercially important species that are sold on ice in the metropolitan centre of Manaus, including tambaqui, arapaima and the common pacu (Santos, Ferreira & Zuanon 2006), are apparently more important in the communities nearer Manaus that receive regular (at least weekly) visits from city-based boats that buy fish and deposit ice. Given the tropical climate and large travel distances from our studied communities of up to ~1500 km to Manaus and ~250 km to the nearest urban centre, some form of refrigeration is essential for the sale of fresh fish to the urban market. The availability and access to ice is regarded as an important determinant of fishing capacity in tropical fisheries in which refrigeration is otherwise not possible (Almeida 2004; Brewer *et al.* 2013). Our data supports and furthers this idea, suggesting that as well as increasing maximum catch biomass, ice availability is an indirect but important driver of catch composition. These results demonstrate the importance of urban linkages and infrastructure in dictating the catch of local fishing-reliant people. They can perhaps partially explain why certain commercially important species of freshwater (Chapter 2), marine (Brewer *et al.* 2009) and terrestrial

(Parry & Peres 2015) wildlife appear predominantly defaunated nearer to centres of urban demand.

The relative importance of fresh fish has increased compared to salted and dried fish throughout the Amazon over recent decades (Garcia *et al.* 2009). Salting fish is a more traditional form of preservation in Amazonia (Mcgrath *et al.* 1993), and is still widely practiced for certain species and in areas without reliable refrigeration (Barthem & Goulding 1997). Three species that explained a lot of the spatial variation in catch (Table S4.5), the silver arowana, the sorubim catfish and the redtail catfish, were mainly caught around more remote communities not regularly provisioned with ice, and are species with an established trade in being sold salted. One of these, sorubim, is known to migrate between 300-500 km (Araújo-Lima & Ruffino 2003), and is therefore potentially threatened by the damming of rivers.

4.5.5. Challenges for management

We identify vulnerable wildlife species (i.e. prone to over-harvesting due to intrinsic vulnerability and /or high harvester preference) that appear to be of high importance during the lean high water season due to the large quantity caught at this time, such as tambaqui fish and several bushmeat species. These species make up a large proportion of the lean season catch, and may not be easily substitutable due to the limited availability of certain species during the flood period. The challenge for management is how to preserve the populations of these species without restricting local people's use during vulnerable times. A further collapse in the populations of such species would probably be detrimental to the nutrition and livelihoods of seasonally vulnerable people. We also demonstrate how the *ribeirinho* utilisation of certain species varies spatially, thereby suggesting that human vulnerability to reduced availability of and access to particular fish species is not homogenous between communities. As such, certain communities may be more vulnerable to threats to the population decline of certain fish species, or to environmental legislation that may reduce access to them.

Amazonian fisheries policy is largely based on restrictions (de Almeida Corrêa, Kahn & Freitas 2014), however, restrictions on access to these resources could have a comparable detrimental impact on harvesters to biological population declines (Adams 2004; Wilkie *et al.* 2006; Sodhi *et al.* 2006; Sodhi 2008). Community co-management (Castello *et al.* 2009; De Mattos Vieira, Von Muhlen & Shepard Jr. 2015; Petersen *et al.* 2016) has seen the most success in natural resource management in the Amazon (Antunes *et al.* 2016). Co-management tends to restrict fishing of important species, but permit sustainable exploitation of fishery resources when populations have recovered. Species co-management programmes could be focussed in areas where local people would most benefit, and factor in heterogeneous sensitivities of communities when implementing legislation which restricts the use of certain species. However, as co-management is currently limited to certain areas, and as it is most successful with non-migratory species (Petersen *et al.* 2016), it is only part of the solution in the expansive Amazon where management resources are highly limited, and many species are migratory.

Migratory fish are particularly vulnerable to dam construction (Araújo-Lima & Ruffino 2003; Duponchelle *et al.* 2016), which is occurring at unprecedented levels in the Amazon. Here, only three free-flowing tributaries are expected to remain in the next few decades if all 277 planned dams are completed (Castello & Macedo 2016). The River Purus remains undammed, and as such this study demonstrates the high importance of migratory catfish (such as the sorubim) to the livelihoods and food security of remote rural communities in undammed rivers. The ability of remote communities to preserve certain species by salting and selling salted fish to an established market offers them an essential livelihood option considering that the lack of infrastructure prevents them from access to the more lucrative fresh fish trade. We therefore suggest that remote riverine communities elsewhere in Amazonia may be vulnerable to dam construction, which could disproportionately impact them through depletion of migratory catfish populations.

4.5.6. Conclusion

In this paper we investigate the community assemblages of fish and terrestrial wildlife species harvested by rural Amazonians, in areas with varying degrees of urban linkages, and during high and low water seasons. We find seasons to have a large impact on species caught, and we consider the potential social implications of this during the high-water fishing lean season, in which the nutrition and livelihoods of local people are highly vulnerable. During this time, harvesters catch more bushmeat, and Muscovy ducks and howler monkeys make up much of the increased catch. Nutritionally and commercially important tambaqui fish are also a large focus of high water harvesting. This presents important challenges to natural resource managers about reconciling the conservation of species and populations with the seasonal vulnerability of local people. It also demonstrates how management can benefit from a greater understanding of specific threats to species that are particularly important to people in vulnerable situations (Dirzo *et al.* 2014), emphasising that the human impacts of defaunation cannot just be measured in kilograms.

4.6. References

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4.7. Supplementary information

4.7.1. Supplementary figures

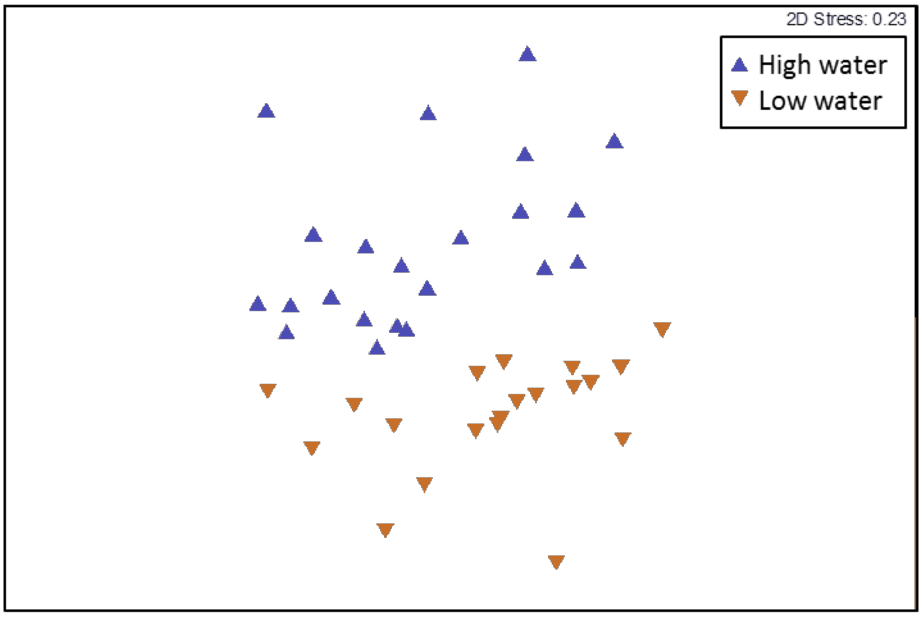

Fig. S4.1. Similarity analysis of seasonal fish assemblages. NMDS (Non-metric Multidimensional Scaling) graphs.

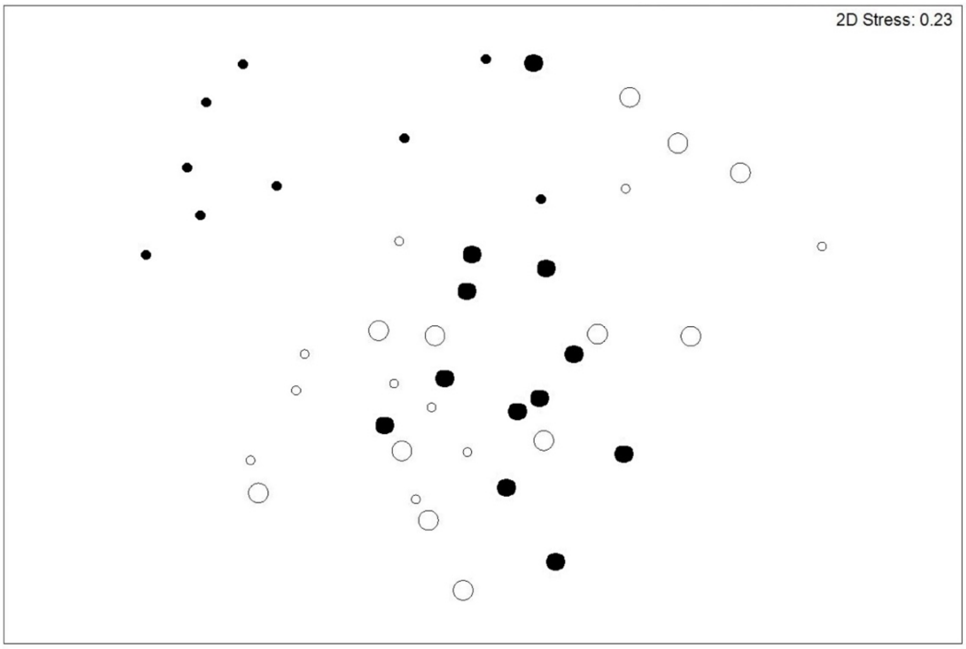

Fig. S4.2. Spatial and temporal similarity analysis of fish assemblages. NMDS graph. Large bubbles are with ice, and small are without. Black bubbles are the low water season, and white are the high water season.

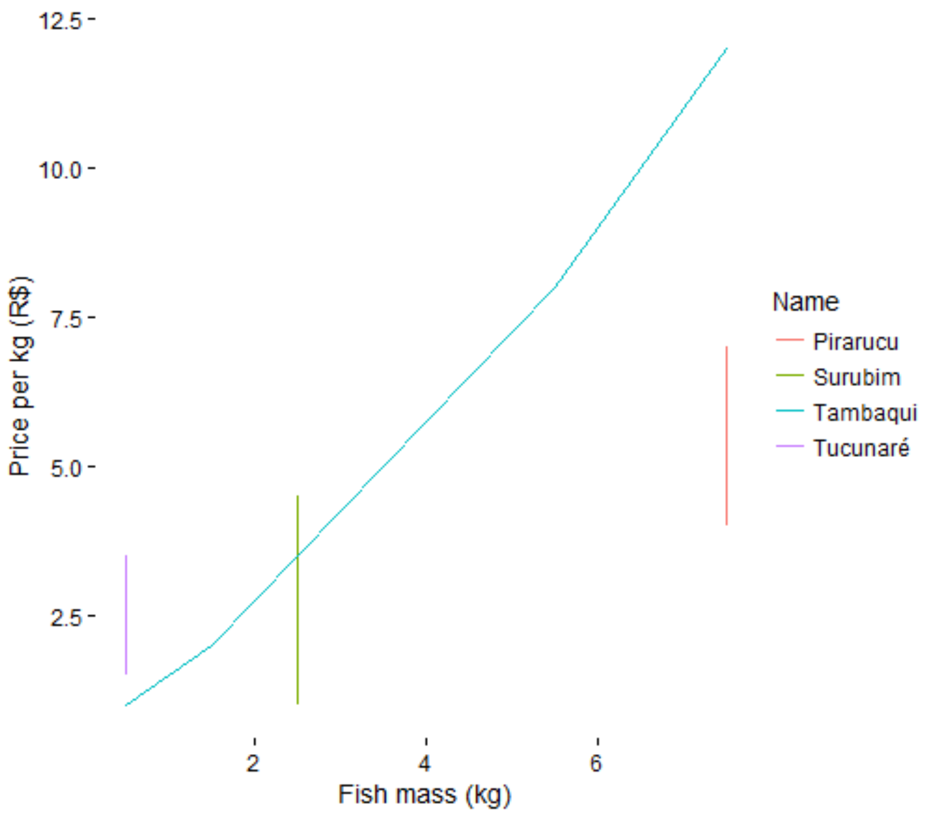

Fig. S4.3. The price-ranges of the four most valuable fish species per kilogram, based on fish-buyer data from the lower River Purus. Data relate to fresh (not salted) fish.

4.7.2. Supplementary tables

Table S4.1. 80 fish taxa summary information. Scientific names, most common local name utilised on the Purus River (personal judgement), and standardised body mass as landed by Purus fishers as calculated and utilised in biomass calculations.

Scientific name	Local name	Body mass (g)
Acestrorhynchus falcirostris	Dente de cão	145.43
Ageneiosus inermis	Mandubé	506.51
Anodus elongatus	Cubiu	42.18
Anostomoides laticeps	Piau sp.	95.15
Arapaima gigas	Pirarucu	25716.84
Astronotus spp.	Cará açu	232.03
Auchenipterus nuchalis	Mandi manteiga	13.57
Brachyplatystoma filamentosum	Filhote	6150.00
Brachyplatystoma juruense	Camisa de meia	536.16
Brycon amazonicus	Matrinxã	481.18
Brycon melanopterus	Jatuarana	308.40
Calophysus macropterus	Piracatinga	158.76
Caquetaia spectabilis	Cará sp.	127.06
Chaetobranchopsis orbicularis	Cará sp.	9.72
Chaetobranchus flavescens	Cará sp.	52.22
Chalceus erythrurus	Arari	72.03
Cichla monoculus	Tucunaré	499.38
Colossoma macropomum	Tambaqui	2733.75
Crenicichla cincta	Jacundá	22.30
Curimata inornata	Branquinha olhuda	94.68
Cynodon gibbus	Cachorro	415.00
Electrophorus electricus	Poraquê	3247.00
Geophagus proximus	Cará roi roi	159.00
Goslinia platynema	Babão	1264.23
Gymnotiformes	Sarapó	195.00
Hemisorubim platyrhynchos	Braço de moça	278.67
Hemisorubim platyrhynchos	Caparari	1962.96
Heros efasciatus	Cará sp.	64.33
Hoplerythrinus unitaeniatus	Jeju	261.33

Hoplias malabaricus	Traíra	621.43
Hoplosternum littorale	Tamoatá	70.05
Hydrolycus scomberoides	Ze d'or	706.24
Hypophthalmus edentatus	Mapará	660.00
Hypselecara temporalis	Cará sp.	48.04
Laemolyta varia	Piau sp.	49.18
Leiarius marmoratus	Jundiá	5635.15
Leporinus agassizi	Piau sp.	81.23
Leporinus fasciatus	Piau flamengo	117.79
Leporinus trifasciatus	Piau sp.	180.70
Lithodoras dorsalis	Bacu pedra	1636.63
Loricaria cataphra	Cari cachimbo	66.51
Megalodoras uranosc	Bacu amarela	1602.42
Metynnis lippincottianus	Pacu galo	20.09
Myleus rubripinnis	Pacu sp.	409.23
Myleus schomburgkii	Pacu burro	908.92
Mylossoma aureum	Pacu branco	175.00
Mylossoma duriventre	Pacu comum	162.35
Osteoglossum bicirrhosum	Aruanã	1625.00
Oxydoras niger	Cuiú	880.00
Unidentified "pacu" sp.	Pacu toba	908.92
Pellona castelnaeana	Sardinhão	1830.52
Pellona flavipinnis	Apapá branco	996.04
Phractocephalus hemioliopterus	Pirarara	3273.45
Piaractus brachypomus	Pirapitinga	2690.48
Unidentified "piau" sp.	Piau manteiga	227.49
Pimelodus blochii	Mandi comum	115.92
Pinirampus pirinampu	Piranambu	1450.00
Plagioscion squamosissimus	Pescada	730.00
Potamorhina altamazonica	Branquinha cabeça lisa	344.12
Potamorhina latior	Branquinha comum	218.31
Potamorhina pristigaster	Peito de aço	249.00
Pristobrycon striolatus/Serrasalmus gouldingi	Piranha branca	93.76
Prochilodus nigricans	Curimatã	492.00

Psectrogaster amazonica	Branquinha cascuda	63.64
Pseudoplatystoma fasciatum	Surubim	2712.93
Pterygoplichthys pardalis (mainly)	Bodó	615.91
Pygocentrus nattereri	Piranha caju	404.00
Rhaphiodon vulpinus	Cachorrão	700.00
Rhytiodus microlepis	Piau pau de nego	123.21
Satanoperca lilith	Cará sp.	186.12
Schizodon fasciatus	Piau comum	227.49
Semaprochilodus insignis	Jaraqui escama grossa	508.83
Semaprochilodus taeniurus	Jaraqui escama fina	238.13
Serrasalmus rhombeus	Piranha preta	781.97
Serrasalmus spilopleura	Piranha olho de fogo	470.00
Sorubim lima	Bico de pato	250.67
Sorubimichthys planiceps	Xinelo	4409.89
Triportheus angulatus	Sardinha chata	94.99
Triportheus elongatus	Sardinha comprida	259.85
Zungaro zungaro	Jaú	6583.33

Table S4.2. Results of DistLM analyses of fish biomass data. These are marginal tests for each variable, applying the Bray Curtis similarity index.

Variables	**Pseudo-F**	**P**	**Prop**
Distance to the nearest town	0.74	0.70	0.02
Distance to Manaus	4.05	<0.001	0.09
Population density	0.51	0.87	0.01
Percentage várzea cover	1.37	0.18	0.03
Season	4.96	<0.001	0.12

Table S4.3. Results of DistLM analyses of fish presence-absence data. These are marginal tests for each variable, apllying the Sorensen similarity index.

Variables	**Pseudo-F**	**P**	**Prop**
Distance to the nearest town	0.41	0.83	0.01
Distance to Manaus	8.20	<0.001	0.17
Population density	0.70	0.62	0.02
Percentage várzea cover	0.32	0.86	0.01
Season	7.96	<0.001	0.16

Table S4.4. SIMPER analysis - Species that contribute most to the between seasons (Bray Curtis), in descending order.

Species	**High water average abundance**	**High water average abundance**	**Average dissimilarity**	**% contribution**	**Cumulative %**
Mylossoma duriventre	23.37	18.41	11.76	14.64	14.64
Pimelodus blochii	16.55	2.84	8.47	10.54	25.18
Colossoma macropomum	15.74	2.23	8.08	10.05	35.23
Triportheus angulatus	1.24	12.10	5.96	7.42	42.66
Osteoglossum bicirrhosum	3.57	10.48	5.52	6.87	49.53
Pseudoplatystoma fasciatum	0.93	11.12	5.51	6.85	56.38
Arapaima gigas	1.23	9.82	5.18	6.45	62.83
Phractocephalus hemioliopterus	1.60	7.28	3.89	4.84	67.67
Triportheus elongatus	2.52	7.46	3.88	4.83	72.50
Pygocentrus nattereri	7.81	0.68	3.70	4.60	77.11
Liposarcus spp.	3.19	5.75	3.57	4.44	81.55
Semaprochilodus insignis	5.59	0.82	2.96	3.69	85.23
Schizodon fasciatus	4.45	2.24	2.58	3.21	88.44
Prochilodusnigricans	2.56	3.12	2.44	3.03	91.48

Table S4.5. SIMPER analysis - Species that contribute most to the dissimilarities between distance to Manaus (Bray Curtis), in descending order

Species	Ice average abundance	Salt average abundance	% contribution	Cumulative %
Mylossoma duriventre	66328	18420	19.17	19.17
Colossoma macropomum	41647	7875	11.08	30.24
Osteoglossum bicirrhosum	20685	44950	9.18	39.42
Arapaima gigas	33607	11500	8.58	48
Pimelodus blochii	655	15822	7.48	55.48
Pseudoplatystoma fasciatum	2522	19290	6.5	61.98
Triportheus angulatus	3523	10461	4.86	66.85
Phractocephalus hemioliopterus	7268	9114	4.61	71.46
Triportheus elongatus	6835	5769	3.82	75.27
Liposarcus spp.	6135	3849	3.61	78.88
Semaprochilodus insignis	3451	4554	3.19	82.07
Cichla monoculus	15338	1199	2.99	85.07
Prochilodus nigricans	12086	3198	2.95	88.02
Pygocentrus nattereri	7606	2141	2.92	90.94

Table S4.6. Results of DistLM analyses of bushmeat abundance data. These are marginal tests for each variable, applying the Bray Curtis similarity index.

Variables	Pseudo-F	P	Prop
Distance to the nearest town	0.22	0.97	0.01
Distance to Manaus	0.66	0.71	0.02
Population density	0.72	0.67	0.02
Percentage *várzea* cover	1.73	0.11	0.05
Percentage *terra firme*	0.66	0.73	0.02
Season	2.70	0.02	0.08

Table S4.7. Results of DistLM analyses of bushmeat presence/absence data. These are marginal tests for each variable, applying the Sorensen similarity index.

Variables	**Pseudo-F**	**P**	**Prop**
Distance to the nearest town	0.29	0.90	0.01
Distance to Manaus	0.34	0.86	0.01
Population density	0.94	0.49	0.03
Percentage várzea cover	**2.57**	**0.03**	**0.07**
Percentage terra firme cover	1.27	0.31	0.04
Season	**2.98**	**0.02**	**0.08**

Table S4.10. SIMPER analysis - Species that contribute most to the dissimilarities between seasons (Bray Curtis), in descending order

Species	**High av. ab.**	**Low av. ab.**	**Av. diss.**	**% contr.**	**cum.%**
Howler monkey	3.05	0.27	14.63	16.62	16.62
Muscovy	2.65	1.80	14.43	16.40	33.02
Other birds	0.90	2.20	13.36	15.07	48.09
White-lipped peccary	0.75	1.33	10.56	12.00	60.09
Curassow	1.15	1.20	8.62	9.79	69.88
Paca	2.35	0.00	8.51	9.67	79.56
Other primates	1.80	0.00	5.88	6.68	86.24
Collared peccary	0.65	0.13	4.19	4.76	91.00

Table S4.11. SIMPER analysis - Species that contribute most to the dissimilarities in *várzea* flooded forest cover (Bray Curtis), in descending order

Species	>50% av. ab.	<50% av. ab.	Av. diss.	% contr.	cum.%
Muscovy duck	2.79	1.18	14.67	16.78	16.78
Howler monkey	2.25	1.00	14.31	16.36	33.14
Other birds	2.00	0.27	12.67	14.49	47.62
White-lipped peccary	1.08	0.82	10.56	12.07	59.70
Curassow	1.54	0.36	8.01	9.16	68.86
Paca	1.63	0.73	7.68	8.79	77.64
Collared peccary	0.33	0.64	5.23	5.98	83.62
Other primates	1.42	0.18	5.06	5.79	89.41
Red brocket deer	0.25	0.36	2.90	3.32	92.73

Chapter 5

“EVERYTHING WE DO IS ILLEGAL”: COMPLEX LINKAGES BETWEEN VULNERABLE NATURAL RESOURCE USERS, THEIR ENVIRONMENT AND LEGISLATION

Left: a black caiman (*Melanosuchus niger*) being skinned, top-right: a giant South American Turtle (*Podocnemis expansa*) turtle caught in a gill-net, bottom-right: processing aruanã (*Osteoglossum bicirrhosum*) fish to be salted. Photo credits: Daniel Tregidgo

"Everything we do is illegal": complex linkages between vulnerable natural resource users, their environment and legislation

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5.1. Abstract

Natural resource users are vulnerable to changes in environmental conditions, markets and legal regulations because these factors dictate returns from extractive activities. In tropical contexts, the diversity of rural livelihoods is important because it influences the capacity of resource-users to adapt to social and environmental change. In this perspective article, we explore widespread concerns voiced by artisanal fishers in the Amazonian floodplain that their livelihoods are being constrained by legislation; optimised by the perception that "everything we do is illegal". Applying a vulnerability framework, we explore the widely held perspective of illegality and contribute new insights into the emerging research area of social-ecological feedbacks. We discuss new evidence of two-way linkages between the vulnerability of rural people and the health of floodplain ecosystems. We show how livelihood portfolios in the Amazon floodplain have historically been constrained by environmental regulations and a collapse in demand for key forest products. In response, the people remaining in these flood-prone rural areas became heavily-dependent on fishing. However, decades of overfishing have led to depressed stocks and many fisheries regulations, further constraining rural livelihood options and exacerbating social vulnerability. Our study also illustrates the complexity of links between the vulnerability of interconnected human, aquatic and terrestrial systems. Specifically, we present evidence that vulnerable rural rainforest people adapt to constraints on fishing by transferring harvesting pressure to sensitive wildlife taxa, including primates and river turtles. We highlight the importance of considering social-ecological feedbacks when managing for conservation or development. In particular, policy-makers should aim to dampen the negative impacts of these feedbacks by incentivising livelihood alternatives that combine with local traditions. In the Amazon, the liberalisation of restrictions on relatively harvest-resilient bushmeat species may facilitate a transition from fishing-only to a more diverse and sustainable harvesting portfolio, and could enhance the capacity of natural resource-users to adapt to stresses on livelihoods.

Key words: adaptive management, fisheries, inter-disciplinarity, livelihood diversification, vulnerability

5.2. Introduction

“Everything we do is illegal” said a frustrated Antonio, echoing a complaint the we (DT and MAR) heard many times on our journey down the River Purus interviewing fishers. Within Antonio’s lifetime rural people had made a living from selling the skins of jaguars (*Panthera onca*) and caiman (namely *Melanosuchus niger* and *Caiman crocodilus*), and until more recently from selectively-logged timber. However, regulatory responses to over-extraction, such as international trade bans on threatened wildlife species and legal restrictions on logging without a formal management plan, have ended these once lucrative livelihood options for people like Antonio. At the same time, many more livelihood activities with lower environmental impacts such as rubber-tapping are no longer economically viable due to market changes (Pyhälä, Brown & Adger 2006; WinklerPrins 2006). Consequently, Antonio currently sees fishing as his last feasible option for making a living, and the enormous demand from the Amazon’s rapidly growing urban centres offers a market for him to sell his catch. Yet his father João, who has lived in the village for 78 years, explained how fishing has become more difficult. He recalled the great abundance of river turtles (namely *Podocnemis expansa* and *Podocnemis unifilis*), and larger species of fish (tambaqui *Colossoma macropomum* and arapaima *Arapaima gigas*) that the river once offered them, telling us that these favoured food species have declined more than any others. It was clear from our conversations about over-exploitation that both men recognise the necessity to regulate harvesting in order to protect stocks. Nonetheless, Antonio was frustrated that his last viable livelihood option, fishing, is being constrained by increasing restrictions concerning species and minimum body sizes, which make much of his catch illegal to sell.

Antonio’s story is not uncommon in the Amazon floodplain, and during structured interviews with nearly 600 fishers, and countless hours of informal discussions, many people expressed similar concerns. The emerging message was that livelihoods have been increasingly constrained by the combination of sustained over-exploitation of natural resources and increased regulatory constraints on livelihood activities. Over-exploitation of natural resources is of great concern both from the perspective of biodiversity conservation, but also for human populations that rely on them to make a living (Milner-Gulland & Bennett 2003; Balmford & Bond 2005). However, management measures to protect natural resources commonly involve the restriction of their use, which inevitably causes at least some disruption to human livelihoods (Adams 2004; Wilkie *et al.* 2006; Sodhi *et al.* 2006; Sodhi 2008; Brashares *et al.* 2011; Cawthorn & Hoffman 2015). Although interventions aim to protect the long-term availability of resources, in the short-term these environmental and institutional use-restrictions cause most harm to human welfare where and when there are limited livelihood alternatives (Cinner & Bodin 2010). In this perspective piece we explore the linkages between natural resources, environmental legislation and resource-users by engaging with the concept of vulnerability: a useful heuristic tool for describing this state of human susceptibility to harm and guiding actions to reduce risk (Adger 2006).

Vulnerability has been defined as the susceptibility to harm from exposure to stresses associated with environmental and social change, and the absence of capacity to adapt (Adger 2006; Smit & Wandel 2006). In Adger's (2006) seminal framework the key parameters of vulnerability are sensitivity, exposure and adaptive capacity. Sensitivity refers to the degree to which harm is likely to be experienced when exposed to a threat. There is evidence that communities strongly dependent on natural resources are highly sensitive to changes in the condition of their resource-base (e.g. fish stocks) (Adger 2000; Marshall *et al.* 2013; Pinho, Marengo & Smith 2015). Wild-meat harvest (wild fish, mammals, birds and often reptiles and amphibians, too) provides an important livelihood activity, and source of protein, fats, energy and micronutrients to billions of people worldwide (Milner-Gulland & Bennett 2003; BNP 2009; Youn *et al.* 2014; FAO 2016). Thus, the livelihood and food security of people dependent on wild meat are highly sensitive to changes in wildlife populations (Allison *et al.* 2009; Béné 2009; Mills *et al.* 2011), especially when and where consumers have limited capacity to switch from wild-meat to domesticated sources of animal protein.

The vulnerability of sensitive social groups such as tropical fishers and hunters (which we collectively refer to as harvesters) to socio-environmental change partially stems from exposure to stresses and shocks that may limit their ability to make a living from wild meat. For harvesters, the reliability of availability and access to wild meat – which could be portrayed as the risk of coming home empty-handed - is inherently variable. Moreover, a harvester's ability to catch, transport or sell wildlife can be compromised by a range of factors including overharvesting (Chapter 2; Cinner *et al.* 2016), seasonal hydro-climatic events (Chapter 3; Endo, Peres & Haugaasen 2016), market fluctuations, and intensification of laws and enforcement (Cinner *et al.* 2011).

Social-ecological vulnerability can occur in a harvesting system when human populations are dependent on exploiting sensitive populations, faunal communities or ecosystems (Fig. 5.1). For example, Golden (2016) estimates that 19% of the global population is vulnerable to nutrient deficiencies in the coming decades as a result of falling marine fish catch. The ability of fishers and hunters to change in order to accommodate stresses such as resource-depletion is known as adaptive capacity (Adger 2006), and is determined by the relative ease of moving away from these constrained activities to successfully adopt alternative livelihoods. This capacity is dependent on social conditions such as governance, civil and political rights, literacy, assets and capabilities (Brooks, Adger & Kelly 2005; Lopes, Silvano & Begossi 2011).

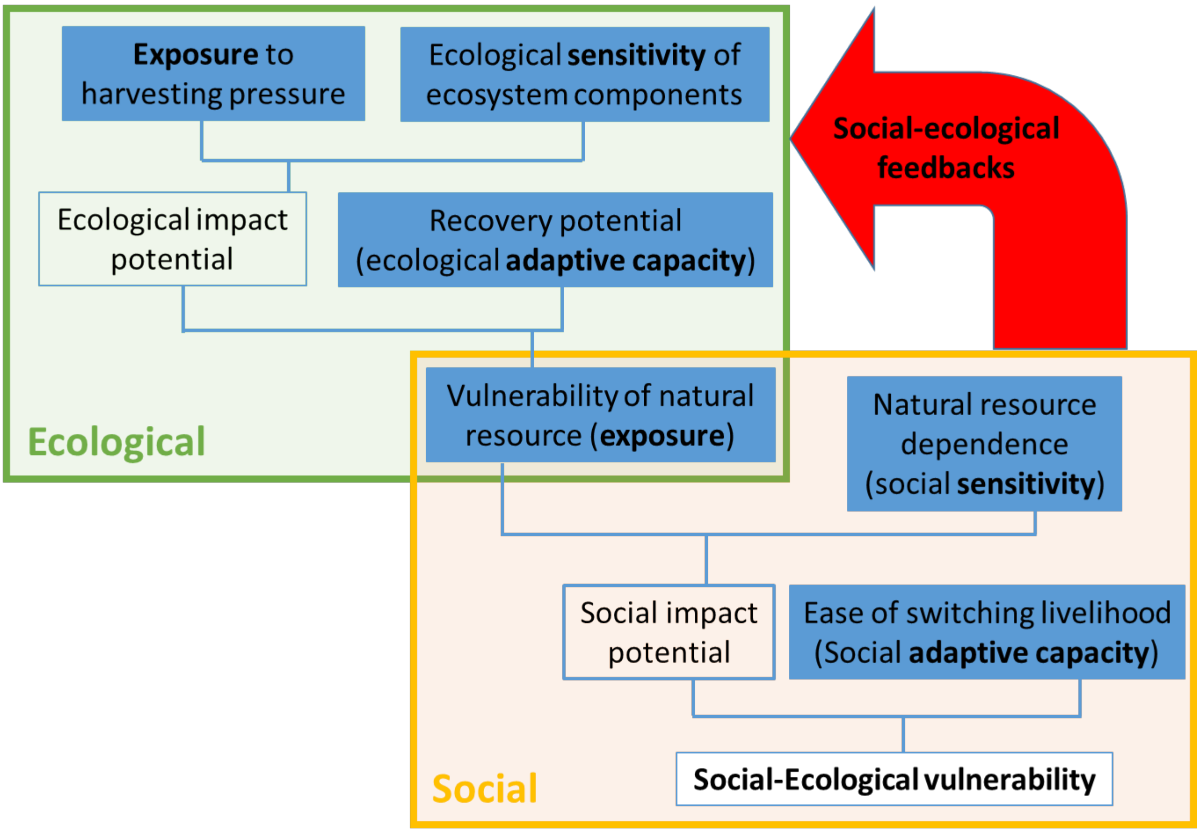

Fig. 5.1. Conceptual framework for understanding linked social-ecological vulnerability. This diagram has been adapted from the general framework of Cinner *et al.* (2013) and Marshall *et al.* (2013) to illustrate a rural context where people are dependent on harvesting natural resources.

Identifying causes and solutions to Antonio's predicament (constrained livelihood choices due to a perception of illegality, as well as an appreciation of the scale and consequences of over-exploitation of the resource base) requires different kinds of knowledges emanating from the natural and social sciences. Despite the endurance of disciplinary research, many natural and social scientists now recognise that ecological and social systems cannot be viewed in isolation (Berkes, Colding & Folke 2008; Castree *et al.* 2014). A major focus of natural science research is understanding anthropogenic environmental impacts (e.g. Dirzo *et al.* 2014). Moreover, there is broad cross-disciplinary interest in the human dimensions of environmental change (e.g. Balmford & Bond 2005; Díaz et al. 2006; Adger 2000), leading to, amongst other things, a growing understanding of how natural resource depletion can impact the well-being of people that are highly dependent on them (Pyhälä, Brown & Adger 2006; Allison *et al.* 2009; Golden *et al.* 2011; Golden 2016; Lam *et al.* 2016). However, social-ecological feedbacks (Fig. 5.1) are poorly understood (Cinner *et al.* 2011; Miller, Caplow &

Leslie 2012; Larrosa, Carrasco & Milner-Gulland 2016). Within a fishery social-ecological system, for example, a feedback might occur if vulnerable people made behavioural changes that amplified or dampened change. In other words, a decline in the catch of an important target fish species could lead to fishing effort and therefore pressure on fish stocks to increase (amplifying response) or decrease (dampening response) (Cinner *et al.* 2011). Similarly, changes in drivers related to climate, governance and markets may shift the focus of fishers to different species, which can alter harvesting pressure on sensitive ecosystem components (Aguilera *et al.* 2015). By recognising the significance of social-ecological feedbacks within fisheries, Cinner et al. (2011) challenge fisheries managers to support livelihoods adaptation in constrained fishers by strengthening dampening feedbacks.

Limited but growing evidence that amplifying feedback responses leave harvesters vulnerable to the social-ecological trap of overexploitation (Steneck 2009; Barrett, Travis & Dasgupta 2011; Brashares *et al.* 2011) offers important warnings for fisheries managers. Fisheries research has made important conceptual and applied advances by identifying such social-ecological feedbacks. However, our understanding of social-ecological feedbacks is still lacking, partly because interdisciplinary social-ecological research tends to focus on a single ecological realm (terrestrial, marine or freshwater). Evidence demonstrates that tropical harvester populations worldwide respond to reduced fish availability by switching to hunting (Brashares et al. 2004; Endo et al. 2016; Chapter 3). These insights into resource substitutability has been discussed mainly in the context of natural resource depletion (Rowcliffe, Milner-Gulland & Cowlishaw 2005), although prey switching has also been considered in the context of optimal foraging theory (e.g. Alvard 1995). However, examining aquatic-terrestrial harvesting interactions through the lens of social-ecological vulnerability could identify additional drivers of resource substitutability and guide subsequent actions to reduce risk of food and livelihood insecurity (Fig. 5.1).

In the Amazon, the world's largest river basin, most of the rural population live in and around the floodplain (Junk *et al.* 2012), and are known as *ribeirinhos*. Social scientists that have explored the vulnerability of *ribeirinhos* have done so almost exclusively in relation to climate change (Brondízio & Moran 2008; Sena *et al.* 2012; Marengo *et al.* 2013; Maru *et al.* 2014; Pinho, Marengo & Smith 2015; Brondízio *et al.* 2016) and dam construction (Queiroz & Motta-Veiga 2012; Rodrigues & Aldemir De Oliveira 2012). The vulnerability of this largely 'invisible' population (Nugent 1993) to environmental and institutional restrictions on natural resources has been largely ignored. This may be because the resource base available for this population has traditionally been seen as highly abundant (e.g. Beckerman 1979), and because the dominant conservation paradigm in the Amazon is forest-centric with little focus on freshwater resources (Castello *et al.* 2013). However, there is recent novel empirical evidence that rural people living in the Amazon floodplain suffer from severe seasonal food insecurity, largely due to low fish catch rates in the high water season (Chapter 3). This seasonal food insecurity emphasises the sensitivity of local people to changes in the availability of fish, despite the great richness of other natural resources in their local environment. Ecologically, the vulnerability of Amazonian terrestrial habitats to social-ecological changes, such as habitat loss and disturbance, are well understood (e.g. Barlow *et al.* 2016). In contrast, freshwater habitats have been less studied, although their major threats have been identified (Castello *et al.* 2013; Castello & Macedo 2016). This paper builds on our current understanding of social-ecological vulnerability by addressing the very poorly understood concerns expressed by Antonio and so many others - can environmental regulations aiming to promote long-term sustainability inadvertently contribute to human livelihood vulnerability?

In this perspective piece, we use open interviews with hundreds of residents of the Amazon floodplain to address this question by examining vulnerability to change in this social-ecological system. Specifically, we examine vulnerability by considering ecological, institutional and market changes; (1) in a historical context in order to understand how have residents of the resource-rich Amazonian floodplain become fisheries-dependent; (2) in the present-day in order to examine how changes to this social-ecological system appear to be constraining fishery-derived livelihoods. We then gather evidence from the literature and conduct open interviews with harvesters about their switching behaviour to ask; (3) how may livelihood vulnerability feedbacks impact ecological vulnerability? We present our perspective of the current social-ecological situation in the Amazonian floodplain based on extensive open interviews with hundreds of local residents, most of which were visited during random sampling for a recent quantitative study (Chapters 2-4). In doing so we voice what we perceived to be widespread concerns of the local population, and discuss them in the context of the wider literature and the vulnerability framework.

We propose management interventions which could dampen negative impacts of social-ecological feedbacks through the diversification of livelihood profiles. Finally, we discuss the broader implications of our findings for natural resource-dependent social-ecological systems, and consider the potential management benefits of taking an interdisciplinary and multi-systemic (i.e. aquatic and terrestrial) perspective.

5.3. Constraints on the floodplain livelihoods profile

In order to understand how an individual's livelihood security may be vulnerable to current and future stresses, we must first recognise how historical events have limited the livelihood options currently available to someone. Many of the world's rural poor are dependent on natural resources either for their principal livelihoods and nutritional source (Sirén & Machoa 2008; Golden *et al.* 2011; López-Feldman 2014; Youn *et al.* 2014; Sarti *et al.* 2015; Golden 2016), or as safety nets when agricultural resources are scarce (de Merode, Homewood & Cowlishaw 2004). People that are highly dependent on a natural resource are therefore very sensitive to perturbations such as defaunation – animal loss from ecological communities - that may impact on that resource or their ability to earn a living from that resource. The poor's access to these resources depends on institutional and social factors, which includes environmental regulations that restrict access to the resource, the activity, or the market to sell it (Ribot & Peluso 2003).

In the context of livelihood vulnerability, adaptive capacity is determined by the relative difficulty of moving away from constrained activities to successfully adopt alternative livelihoods (Brooks, Adger & Kelly 2005; Lopes, Silvano & Begossi 2011). Livelihood diversification is essential for achieving the capacity to adapt to constraints on livelihoods caused by social and environmental changes and is considered a key strategy to being resilient to risks (Marschke 2006; Cinner & Bodin 2010; IFAD 2010; Aguilera *et al.* 2015). This diversification is also the process by which a broad portfolio of activities are constructed in order to survive, and improve their standards of living (Ellis 1998). Livelihood diversification is common in response to shocks globally (Ellis 1998; Allison & Ellis 2001; Cinner & Bodin 2010), and the vulnerability of the rural poor could be exacerbated if livelihood options are constrained. In this section we explore how, despite resource richness, a suite of social and institutional factors has constrained livelihoods in the Amazon floodplain since the demise of the rubber boom(s) (c.1912 and then again post WWII), leading to the current reliance on fishing. These factors include international competition reducing market demand for Amazonian products (e.g. rubber and jute), trade bans on overexploited keystone species (e.g. pelt trade), and increased legislation and enforcement to counter deforestation (especially around roads) following logging and agricultural expansion.

5.3.1. Rubber

Amazonia's human geography was transformed by the 'rubber boom', which began in the 19th century. Around half a million people migrated to the region from other parts of Brazil to earn a living from tapping wild rubber (*Hevea brasiliensis*). Although only traders – rather than tappers – prospered, at its peak Amazonian rubber represented 40% of Brazil's export revenues (Dean 1987). A fall in rubber prices due to the expansion of more productive Southeast Asian plantations ended the Amazonian rubber boom in the early 20th century. However, during World War II the Japanese blocked Asian rubber supplies, leading to further migration of 35,000 – 80,000 'rubber soldiers' into Amazonia to tap rubber for the US market (Dean 1987). Post-war rubber prices crashed once again, leading to the departure of many rubber-tappers and the impoverishment of the hundreds of thousands of remaining tappers and their families. In the last quarter of the 20th Century, away from the new highways and settlement projects, many river-dwelling rubber-tappers were forced to diversify their livelihoods through earning a living largely by selling a number of alternative river and forest products to river traders (*regatões*) (Mcgrath 2004). Today most rubber produced is synthetic, and prices are very unlikely to rebound. Some rural Amazonians still earn a living from rubber tapping, however the low price earned means that the activity is only economically viable when subsidised (Kugel & Jha 2013).

5.3.2. Other non-timber forest products

Non-timber forest products (NTFPs) were strongly advocated in the 1990s as a mechanism for sustainable development in rainforest nations (Myers 1988; Panayotou & Ashton 1992; Plotkin & Famolare 1992). However, despite the potential of Amazonia's many other NTFPs as livelihood sources, market commercialisation is not always possible, and their sale represents only a safety net activity and supplementary income source for most people (Pyhälä, Brown & Adger 2006). Substitution through domestication abroad and synthetic production has led to the decline in the value of other NTFPs. For example, the fibre Jute (*Corchorus* spp.) was the main cash crop in much of the Amazon for many decades. However the collapse of the jute trade can largely be blamed on competition from cheaper synthetic fibres and from lower-cost Bangladeshi producers (Smith *et al.* 1995; WinklerPrins 2006).

5.3.3. The fur trade

The international trade in animal hides and pelts was minimal until the rubber collapse, after which hunting and trading wildlife offered an important substitute product for enterprises, and alternative livelihood option to many Amazonians. Previously, overexploitation of wildlife in Amazonia was largely based on the regional trade in turtles for cooking oil and lighting (Smith 1979), and in manatee (*Trichechus inunguis*) for their skins and meat (Domning 1982). Antunes et al. (2016) conservatively estimate that 23.3 million wild mammals and reptiles were commercially hunted from 1904 to 1969, with hides and pelts becoming the second most traded Amazonian extracted products after rubber during World War II. Heavily exploited species included peccaries (*Tayassu pecari* and *Pecari tajacu*), red brocket deer (*Mazama americana*), ocelots (*Leopardus pardalis*), jaguar, capybara (*Hydrochoerus hydrochaeris*), giant river otters (*Pteronura brasiliensis*), and black caiman (*Melanosuchus niger*). The pelt trade was pushing many species, such as the giant otter, towards extinction. Much of the impetus to conserve species came from international pressure and environmental legislation. Important roles in the abatement of the threat from the pelt trade came from CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora), which was ratified in 1975 and the enforcement of which was improved in the 1980s, and from the 1992 Rio Convention on Biological Diversity, which helped build global awareness of the issue (Swank & Teer 1989; Antunes *et al.* 2016). While hunting continues today largely for subsistence purposes, these regulations have reversed the decline in many overhunted species, but hence also ended pelt-sale as a widespread livelihood option for rural Amazonians.

5.3.4. Timber

Logging restrictions were largely intended to prevent large-scale road-based logging linked to agricultural expansion along the Amazonian deforestation frontier, but *ribeirinho* livelihoods earned from often much smaller-scale timber extraction have now become limited as a result. *Ribeirinhos* have long participated in highly selective logging for subsistence needs (e.g. for building houses and canoes) and for cash income, which has occurred on a much smaller scale than capital-oriented deforestation that is often associated with agricultural expansion. The Amazon contains billions of cubic metres of tropical hardwoods, which have provided timber to meet demands of markets in Amazonia (11%), the rest of Brazil (53%) and abroad (36%; from 2004 data; Lentini et al. 2005). Logging and industrial timber processing employed an estimated 5% of the economically active population (344 thousand people) of the Brazilian Amazon in 2004 (Lentini, Veríssimo & Pereira 2005), when Amazonian deforestation was at its peak. Since then, the annual rate of deforestation in the Brazilian Amazon has fallen by around 70%, a fall which can largely be attributed to the expansion of protected areas, and the implementation and enforcement of Brazil's forest code, which now requires landowners in the Amazon to maintain 80% of forest cover as legal reserves (Nepstad *et al.* 2014).

5.3.5. Present day livelihood options

The fall in demand for Amazonian products was caused largely by market trends, and the rise in restrictions on harvesting timber and animals due to overwhelming evidence of threats to habitats and species. This has caused the loss of some rural Amazonians' once most common and lucrative livelihood options. Widespread timber and NTFP extraction has been replaced by alternative livelihood activities that predominate in the in the Amazonian floodplain today. Although most traditional income sources are now relatively insignificant, there is one notable exception: açaí fruit (*Euterpe oleracea*) brings large revenues to certain areas. However, the commercial açaí harvest is concentrated around major centres of urban demand, and has led to intensification and plantations (Brondízio 2008). Most rural Amazonians also plant food crops, including manioc, pumpkin, watermelon and corn, for subsistence and sale of any surplus (Dufour *et al.* 2016). However, in many areas, including the floodplain, agriculture now makes a relatively modest contribution to average households cash income (Chapter 2, Fig. S2.5). Instead, alternative sources of monetary income have also become increasingly important. Salaried jobs are rare in rural areas, and largely restricted to teachers and health workers. Today, conditional cash transfers (CCTs) provide many rural households with their major source of monetary income (Chapter 2, Fig. S2.5). The most important of these to *ribeirinhos* have been the *defeso* fishing closed season payment, pensions, and the *Bolsa Familia* family welfare payment. However, the most common livelihood activity that provides *ribeirinho* households with the majority of their earned income is fishing (Chapter 2, Fig. S2.5), and that will be examined next.

5.4. Over-exploitation of key fish stocks in Amazonia

As well as being the principal livelihood option, there is strong evidence that fish also provides the inhabitants of the floodplain with their primary source of protein, secondary source of calories, and a major source of many essential micronutrients (Murrieta & Dufour 2004; van Vliet *et al.* 2015; Dufour *et al.* 2016; Endo, Peres & Haugaasen 2016; Chapter 3). Because the rural Amazonian population is so reliant on fish for their livelihoods and nutrition, their material well-being and health is also likely to be sensitive to exposure to threats to this essential asset; fish stocks. Dam construction, pollution, deforestation and overfishing are among the greatest threats to Amazonian freshwater ecosystems, and therefore fish populations (Castello *et al.* 2013).

5.4.1. Defaunation threatens livelihoods

The livelihood security (Lam *et al.* 2016) and food security (Golden 2016) of fishing-reliant populations are vulnerable to declines in fish catch. Importantly, the potential impacts of threats such as overfishing are more severe to certain sensitive components of the fish community. As such, species compositional changes are primarily observed in depleted fisheries, while catch is often initially maintained through increases in effort, and a shift of effort to less exploited populations (Vestergaard 1996; Pauly *et al.* 1998; Allan *et al.* 2005; Watson *et al.* 2013). Among *ribeirinhos* much of the variation in fish catch composition is explained by distance to large urban markets (Chapter 4). In particular, species with high commercial value (Fig. S4.3), which are sold fresh (on ice), make up a greater proportion of the catch biomass near the metropolitan centre of Manaus compared to more remote rural communities. Riverine communities nearer Manaus have access to ice for refrigeration, and regular city-based fish buyers, which are required by many fishers to maintain a living from selling fresh fish (Chapter 2). Many of the remote communities that lack refrigeration are reliant on salting as a principal method of fish preservation, and the Amazonian salted fish trade is dominated by catfish. Remote rural communities on the un-dammed River Purus still rely heavily on the trade in catfish (Chapter 4). For the many Amazonian watersheds with dams (Castello & Macedo 2016; Winemiller *et al.* 2016), remote rural communities are clearly vulnerable to catfish declines because dams inhibit migrations (Araújo-Lima & Ruffino 2003; Duponchelle *et al.* 2016).

Rural communities nearer to large urban markets tend to be reliant on commercially valuable fish species and thus may be particularly vulnerable to defaunation driven by commercial overfishing (Fig. 5.1). The fish species that earn Amazonian fishers the greatest price per kilogram are several large-bodied species that are most commonly sold fresh, and are hence most important where refrigeration (ice) is available (Chapter 4) and travel distances are shorter. The financial return (value) from fishing per unit of effort (VPUE) is dependent on fish catch rate (catch-per-unit-effort: CPUE) and the per unit price of the fish caught, dictated by fish species and size class (Fig. S4.3). Many factors influence prices, but the most commercially valuable fishes per unit weight tend to be larger species and size classes. Large-bodied fish are also often the most sensitive to fishing pressure due to their slow-growing nature and large range sizes (Fig. 5.1), which is why the loss of large fish is a classic first sign of fishery collapse (Allan *et al.* 2005). In the Amazon, the mean maximum total length of fished species has reduced from 206cm in the early 1900s to 76cm today

(Castello *et al.* 2013). The most valuable of all Amazonian fish is the favourite species of both rural (Chapter 2, Fig. S2.7) and urban consumers (Chapter 2, Fig. S2.8); tambaqui. The market demand for tambaqui from Manaus has been blamed for the species' decline, indicated by a reduction in body size and CPUE that is most intense closer to the city where city-based boats are frequent visitors to rural communities (Chapter 2). Hence the threat to livelihoods is caused by a combination of decreased CPUE and lower price per kilogram that fishers earn for smaller size classes (Fig. S4.3), resulting in a much lower VPUE. This may reduce the ability of people to earn a living from fishing, particularly in the lean fishing season (Chapter 3) when tambaqui contributes a particularly important part of the catch (Chapter 4).

5.4.2. The flooded forest

The ecology of the Amazonian flooded forest is closely linked with social vulnerability due to the importance of the flooded forest as a fish feeding habitat for important food species, and because the high-water season is characterized by poor-fishing, food insecurity and greater hunting effort (Chapter 3). Defaunation of fish populations also results in cascading impacts onto ecosystem function (Allan *et al.* 2005; McCauley *et al.* 2015). The declining body size of commercially important frugivorous Amazonian fish (such as tambaqui; Chapter 2) is of particular concern because larger fish are more effective seed dispersers, and some larger seeds can only be dispersed by larger fish. The defaunation of large frugivorous fish therefore inhibits ecosystem function (Correa *et al.* 2015; Costa-Pereira & Galetti 2015) and hence forest recovery potential (ecological adaptive capacity). It does so by inhibiting frugivorous fish dispersed seed species (particularly larger seed species) to germinate successfully, colonize unoccupied and distant patches and maintain gene flow across fragmented plant populations (Anderson, Rojas & Flecker 2009; Anderson *et al.* 2011; Correa *et al.* 2015).

In summary, fishers are increasingly vulnerable to defaunation of their principal asset - fish - thereby constraining their fisher-derived livelihoods. In the Amazon, urban centres provide the principal market for fishers to sell their catch, through which they earn a living. However, highly selective demand from the same urban centres is also responsible for the overfishing-driven depletion of some of the most commercially and ecologically important fish species. These urban-driven processes may be most intensive near urban centres, yet more remote communities often lack refrigeration and may suffer disproportionately from threats that specifically impact on fish species that have an established market in being sold salted, such as the impact of dams on migratory catfish. The evidence we present in this paper echoes the views of *ribeirinhos*, who perceive that fishing, particularly of larger commercially-important species, has become increasingly difficult.

5.5. Regulatory responses to over-fishing constrain livelihoods

Overfishing is a major cause of marine and freshwater defaunation worldwide (Allan *et al.* 2005; McCauley *et al.* 2015; Young *et al.* 2016). Fisheries management responds to overfishing-induced defaunation through measures including gear or effort restrictions, quotas, fishing closed periods, and no-fishing areas, which aim to protect fishery resources, and therefore the fishers that rely on them (Allison & Ellis 2001; Lopes, Silvano & Begossi 2011). However, healthy fish stocks are of little use to a fisher without access to them, and fisheries management can therefore constrain fisher livelihoods (Tuler *et al.* 2008). The adverse impacts of fishery regulations on fishing communities are increasingly being recognised through, for example, the obligatory employment of social impact assessments in the US, that can evaluate impacts of regulations on resource users (Tuler *et al.* 2008). In social-ecological systems worldwide there has been a shift towards increased participation of local people in natural resource management, one of the goals of which is to consider social impacts of management (Berkes 2004). This is certainly true in the Amazon flooded forest, however Castello, Viana & Pinedo-Vasquez (2011) argue that local knowledge has generally been poorly integrated into management, with the socio-economic and political invisibility of *ribeirinhos* having been highlighted in the past (Nugent 1993), and in other resource management scenarios such as fire management (Carmenta *et al.* 2013).

Understanding community perceptions of the management performance of social-ecological systems is essential for integrating local communities into management (Delgado-serrano *et al.* 2015). The common perception of *ribeirinhos* that "everything we do is illegal" is partly explained by the historical context given earlier in this paper, which describes how restrictions and markets have constrained previously important extractive livelihood activities.

There has been a decline in landed mean fish body sizes across the Amazon (Castello *et al.* 2013) and increasing restrictions on the size and species that can be legally sold. These are the impacts of environmental and institutional changes, and together serve to decrease the rights-based access of fishers to much of the Amazonian fishery (Ribot & Peluso 2003). However, without any fisheries management it is likely that fish stocks would be in a much worse state, and there is some evidence of fisheries recovery in response to management in the Amazon (Almeida, Lorenzen & Mcgrath 2002; Silvano, Ramires & Zuanon 2009; Petersen *et al.* 2016). Fishing policy in the Amazon is based on restrictions on when a fish can be caught, the type of gear that can be used, and the size and species of fish that can be sold (de Almeida Corrêa, Kahn & Freitas 2014). Minimum size limits are placed on several species with the intention of protecting juveniles, and maintaining reproductive success (Ruffino 2004). For example, the minimum size limit of tambaqui is 55 cm in length. However, commercial overfishing has resulted in a reduction in tambaqui body size, leading to the mean fished individual to be a fraction of the legal minimum size (Chapter 2), with as little as 1% of local fishers' catch meeting the legal size limit (Garcez Costa Sousa & de Carvalho Freitas 2011). Consequently, the minimum size regulation makes much of the tambaqui caught from stocks of reduced sized individuals illegal to sell. However, with few viable options for livelihood diversification, the strong urban demand (Chapter 2, Fig. S2.8), high price received (Fig. S4.3) and lack of effective enforcement (de Almeida Corrêa, Kahn & Freitas 2014), catching and selling illegally sized tambaqui remains an attractive option.

Our analysis of fishing demonstrates that fishery-dependent *ribeirinhos* are vulnerable to a 'perfect storm' of overfishing-mediated defaunation and resulting environmental regulation, and limited capacity to adapt due to a reduced livelihood portfolio. Their nutritional vulnerability is evidenced empirically through severe seasonal food insecurity, demonstrating insufficient adaptive capacity to avert harm during periods of low fish availability.

5.6. Unintended outcomes of regulation through social-ecological feedbacks

Vulnerable wildlife harvesters may respond to constraints on their harvesting activity by switching harvesting pressure to another taxon. In west Africa, Brashares et al. (2004) demonstrated that bushmeat hunting increases in years of poor fish supply. In the Amazon floodplain it appears that the fall in fish catch during the high-water lean season cannot be offset by alternative food sources to avoid food insecurity (Chapter 3), and rural Amazonians increase hunting effort (Chapter 3) and bushmeat harvest (Endo et al. 2016; Chapter 4) during the high water lean season. This unique empirical evidence of low fish catch rates coinciding with severe food insecurity and increased bushmeat offtake exemplifies how human vulnerability may cause ecological vulnerability via social-ecological feedbacks (Fig. 5.1).

Given that the increased hunting pressure appears to be caused by overfishing-driven depletion (Brashares *et al.* 2004) and seasonal changes in fish catch rates (Endo, Peres &

Haugaasen 2016; Chapter 4), we suggest that such a switch may be caused by anything that increases the vulnerability of resource-users by constraining their ability to make a living from fishing. For example, an increase in hunting pressure could be an indirect impact of dam construction. We argue here that fisheries restrictions on specific target species may result in similar switching behaviour to other species, a notion we support with anecdotal evidence from the central Brazilian Amazon. Until recently Marcelo (not his real name), like many fishers on the River Purus, principally made their living from the piracatinga (*Calophysus macropterus*) fishery. Piracatinga fishing has recently been banned (Franco *et al.* 2016), in response to evidence that fishers commonly used pink river dolphin (*Nia geoffrensis*) or caiman as bait to catch them (Brum *et al.* 2015). Marcelo told us that he now earns his livelihood largely from the sale of highly lucrative but threatened turtles. Although the sale of both piracatinga and turtles are illegal, the active local market in turtles (Pantoja-Lima *et al.* 2014) probably makes law evasion easier than that of piracatinga. The market for piracatinga is more focussed on larger urban areas and abroad (principally Colombia) (Brum *et al.* 2015), thereby requiring traders to navigate municipalities containing large urban areas and with international borders, which have higher environmental law enforcement capacity (Swan 2016). Hence, well-intentioned actions to protect the pink river dolphin are likely to have displaced some harvesting pressure onto other vulnerable taxa. In a similar way, rubber tappers in Amazonian extractive reserves have become increasingly dependent on cattle ranching (Salisbury & Schmink 2007). These examples demonstrate the importance of carrying out monitoring of the effectiveness of management and regulations, including assessments of any perverse consequences of restrictions that constrain or change livelihoods.

In summary, we have drawn on our own qualitative evidence from research conducted in the Amazon floodplain, combined with empirical insights from other systems, to outline how restricting harvest of one taxon can result in a substitution of effort to another. We elucidate how substitution can result in perverse ecological consequences for sensitive wildlife populations. To limit both social and ecological vulnerability, management must consider the adaptive capacity of harvesters with more flexible restrictions that permit local people to develop a large livelihood portfolio, thereby permitting livelihood diversification to options that are viable to their subsistence and which are ecologically sustainable. It is vital that future research can help understand how management of one component of the system can avoid negatively impacting on another.

5.7. Can rural livelihoods be diversified to reduce social-ecological vulnerability?

Diversity is an important positive attribute of rural livelihoods in developing countries (Allison & Ellis 2001). In constructing a diverse portfolio of activities (livelihood diversification), rural people may improve livelihood security. For example, a fishing community with good options for livelihood diversification may be relatively unaffected by constraints on fishing, which may instead lead to a new social organisation in which other extractive activities become more important than fishing (Lopes, Silvano & Begossi 2011). Hence, the ultimate effects of fisheries regulations on fisher vulnerability depend on existing ecological and social conditions that govern adaptive capacity (Lopes, Silvano & Begossi 2011).

5.7.1. Vulnerability to policy change

Livelihood and income diversification are important in adapting to social and environmental changes (Smit & Skinner 2002; Szlafsztein 2014), and where fishing is restricted to achieve management goals it is essential to have alternative sources of income and nutrition (Johannes 2002). Un-earned income sources in *ribeirinho* communities have increased in recent decades, indeed the main sources of monetary income to most *ribeirinho* households are now CCTs (Fig S5.1). These CCTs have succeeded in reducing poverty and food insecurity, with Brazil's *Bolsa Familia* programme being credited with helping to lift 36 million people out of income poverty (Tepperman 2016). However, a dependence on CCTs makes *ribeirinhos* sensitive to policy changes that impact upon them (Lemos *et al.* 2016). This has been the case with Brazilian fishers, who in 2016 experienced major uncertainties and policy changes regarding the *defeso* fisheries closed season payment (Cruz & Alegretti 2016; Oliveira 2016; Ramalho 2016) and the *Bolsa Familia* payment (Mariz 2016), both of which are expected to see reductions in the number of recipients and quantity received. The capacity for fishers to adapt to losses in welfare payments through fishing or alternative extractive activities in the light of so many constraints on their income sources is therefore limited.

5.7.2. Policy should build adaptive capacity

Policy should enhance the capacity of social-ecological systems to adapt, particularly where they are unstable and prone to experiencing change. Policy interventions often aim to control change in social-ecological systems, rather than managing the capacity of systems to cope with, adapt to, and shape change (Folke 2006). Instability and uncertainty in the Amazon flooded forest is demonstrated through evidence that fish populations have been declining for decades despite years of restrictions (Chapter 2, Petrere Jr. 1986), intensifying and less predictable hydrological events (Marengo *et al.* 2013), and a history of changing income sources for residents exacerbated by political turmoil during and proceeding Dilma's presidency. We argue that through the restrictions placed on fishing and other livelihood activities, environmental management in the Amazon is inhibiting the capacity of local people to adapt to changes rather than building this capacity. In a social-ecological system facing such rapid changes and uncertainty, adaptive management, in which decision making is influenced by continual learning about changes within the system, is essential. Encouragingly. management that considers human vulnerability by reducing dependence on fishing (sensitivity), and increase alternative livelihood options (adaptive capacity) is increasingly being implemented, albeit on a small scale and in select areas of the Amazon.

Maintaining diverse livelihood portfolios has been facilitated in Extractive and Sustainable Development Reserves, which permit Amazonians to continue sustainable traditional livelihoods. The large-scale expansion of reserve coverage that has occurred in recent decades in Amazonia therefore provides an opportunity to decrease social-ecological vulnerability through continued and increased encouragement of livelihood diversification (Lopes, Silvano & Begossi 2011).

Conservation efforts by governments and environmental organizations often try aim to reduce the occurrence of environmentally harmful activities by replacing them with alternative livelihoods that offer social benefits with minimal environmental impacts. However, providing alternative livelihoods may not result in a substitution away from environmentally damaging activities, as people's struggle to escape poverty means that they will always opt to leave unreliable income sources (Salisbury & Schmink 2007; Torell *et al.* 2010; Bauch, Sills & Pattanayak 2014; Wright *et al.* 2016). Such interventions are particularly unlikely to be effective if they are based on efforts to shift local values (Manfredo *et al.* 2016). Consequently, alternative activities that have traditionally been employed, such as banned but once-lucrative wildlife trading, may offer the best chances of success.

5.7.3. Liberating the trade in harvest-tolerant wildlife species

During conversations concerning the constraints imposed by environmental restrictions on the River Purus, resource-users regularly suggested that if something is banned, something else should be liberated. While it would be scientifically-unsound to liberate the harvest of another endangered and vulnerable species, it is perhaps worthwhile re-examining the case for liberalising the harvest of relatively abundant and harvest-tolerant species with a history of extractive use. After all, it is inconsistent that, at least in the Brazilian Amazon, regulation of fishes is highly-specific to population pressures and trends, whereas there is an outright ban on any trade in all species of wild mammals and birds. Indeed, Rowcliffe, Milner-Gulland & Cowlishaw (2005) argue that bringing the currently illegal trade in harvest-tolerant species into the formal economy could provide the incentive needed to monitor and manage stocks effectively, and others argue that this could improve protection of vulnerable species (Brown & Williams 2003; McAllister, McNeill & Gordon 2009; Weber *et al.* 2015; Torres *et al.* 2016). For example, some species involved in the bushmeat trade can tolerate high hunting pressures due to high intrinsic rates of population increase and their ability to live in human-modified systems. Hence, various authors suggest that more resistant species such as cane rats (*Thryonomys* spp.) (Cowlishaw, Mendelson & Rowcliffe 2005), blue duiker (*Cephalophus monticola*), African brush-tailed porcupine (*Atherurus africanus*) (van Vliet & Nasi 2008) and paca (*Cuniculus paca*) (Parry, Barlow & Pereira 2014) could be sustainably exploited to meet demand in African and Amazonian bushmeat markets.

Amazonian livelihood diversification could include permitting and facilitating the sustainable exploitation of alternative resilient environmental resources that have been banned. For example, legalised harvest of peccary leather used in the manufacture of luxury gloves and shoes for the international market brings significant socio-economic and conservation benefits to parts of the Peruvian Amazon (Bodmer, Lozano & Fang 2004). Even prominent international conservation NGOs - including WWF - now advocate controlled sustainable trade in species previously threatened by overharvesting as important for wildlife conservation and livelihoods (Roe 2008).

5.7.4. Widespread sustainable caiman trade?

Could there be a sustainable harvest of caiman in Amazonia? There is a long history of caiman exploitation in Amazonian floodplains (Marioni, Arias & Sinomar 2013), making it an alternative livelihood option that combines well with existing local practices. We heard regular accounts of human-caiman conflict whereby incidences of caiman tearing fishing nets (sensu Peres & Carkeek (1993)) or perception of danger led to local people killing caiman, often without utilising their meat or skin. Furthermore, local people regularly suggested that a legal caiman trade would be a good alternative. Caiman became overexploited before their trade was regulated in the 1970s. In response to continued illegal activity, international restrictions were loosened in 2007 in order to permit some controlled legal trade in the black caiman (*Melanosuchus niger*), by moving it from CITES Appendix 1 to 2. In the Brazilian

Amazon the illegal unregulated caiman meat trade has become widespread in the past few decades (Mendonça *et al.* 2016). Legal caiman hunting is permitted in few Sustainable Development Reserves under strict population monitoring regimes (Botero-Arias & Regatieri 2013), yet Brazil lags behind other South American countries in this respect (Marioni, Arias & Sinomar 2013). National caiman management programmes have seen successes in Venezuela and Bolivia where large quantities of caiman have been sustainably hunted and exported with no evidence of detrimental effects on wild populations (Da Silveira & Thorbjarnarson 1999; Thorbjarnarson & Velasco 1999; Velasco *et al.* 2003). Local livelihoods appeared to have also benefited, for example, in Bolivia the caiman leather trade employed 1,750 people (Burgener 2007), with most income going to indigenous populations (Aparicio & Ríos 2006).

In recent decades management of the Amazonian social-ecological system has actively demonstrated recognition of considering both biodiversity and human livelihoods. It has done so through the expansion of Extractive and Sustainable Development Reserve establishment (Lopes, Silvano & Begossi 2011), community co-management of wildlife populations (Petersen *et al.* 2016), and legalising the trade in previously protected caiman (Marioni, Arias & Sinomar 2013) and peccary (Bodmer, Lozano & Fang 2004), albeit on small scales. Although such initiatives provide some optimism for the future, their benefits may be spatially restricted to a few heavily-managed areas. Advocates of wildlife trade liberalisation emphasise the extreme caution that must be exercised when altering protective wildlife legislation, and the importance of population monitoring and strict population management (Marioni, Arias & Sinomar 2013). However, as sustaining existing monitoring programmes is already threatened by limited resources (Marioni, Arias & Sinomar 2013), the challenge is how to expand such capacity-building in order to promote diversification of culturally-relevant livelihood options such as caiman hunting throughout the Amazon basin, and in other social-ecological harvesting systems throughout the world (Roe 2008). In achieving this, livelihood diversification could increase the capacity of people to adapt to change, whilst reducing pressures on fish stocks.

5.8. Conclusion

This paper was motivated by eight months of detailed social fieldwork in 22 communities along 1267 km of the River Purus. During this time, we encountered the widespread concerns among Amazonian fishers that environmental and institutional changes have meant that making a living from fishing is becoming increasingly difficult, and that there are few viable alternatives. In assessing the vulnerability of the Amazonian floodplain social-ecological system, we discuss evidence that historic market and institutional stresses have created a high present dependence on fishery-based livelihoods. It appears that fishing is now being constrained by the almost inevitable defaunation that overfishing-has caused, and resultant increased fishery restrictions. By applying Amazonian and global evidence of harvester switching behaviour to other sensitive taxa in response to constrained fishing, this paper contributes to the poorly understood concept of social-ecological feedbacks (Cinner *et al.* 2013a; Larrosa, Carrasco & Milner-Gulland 2016), in which social vulnerability can increase ecological vulnerability. The recognition of these feedbacks as part of the social-ecological systems framework demonstrates the complex linkages between, not only social and ecological systems, but also aquatic and terrestrial ecosystems. By applying this framework to management considerations in our study system, we believe that the view expressed by local people, that increasing fishing restrictions should be met by the relaxing of regulations on the extraction of other natural resources, should be contemplated as a way of reconciling conservation and development aims. Considering social-ecological feedbacks, we argue the importance of diversifying rural livelihoods to match local practices and capabilities in reducing the vulnerability to natural resource users and the natural resources themselves.

5.9. References

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Chapter 6

GENERAL CONCLUSION

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6.1. Key findings

The aim and motivation of this thesis was to better understand the complex linkages between biodiversity conservation, rural livelihoods and food security in the Amazonian floodplain. The focus of my empirical research has been the rural riverside (*ribeirinho*) communities of the Amazon floodplain. In these places, wildlife harvest provides rural people and the region's rapidly growing urban centres with much of their animal protein, largely in the form of fish. Through an analysis of lifetime fishing activities recalled by *ribeirinhos*, in Chapter 2 I show that urban demand from the Amazon's largest city of over 2 million people drives wild fish defaunation over 1000 km into remote rainforest areas. Fish price and seed dispersal data suggest negative consequences of this defaunation for local incomes and flooded forest diversity. In Chapter 3 I reveal severe seasonal food insecurity among *ribeirinhos*, although interestingly I found no spatial associations of food insecurity with the defaunation detected in Chapter 2. Through linking measures of food insecurity and wildlife harvest, this thesis also provides novel evidence that food insecurity can result from falls in wildlife catch rates (Chapter 3), and can drive increased bushmeat offtake (Chapter 4). In addition to biomass trends, I also show in Chapter 4 how seasonal and market forces can dictate wildlife harvesting profiles. By interacting, working and living with local people I was also able to make important insights into their lives and worries, which allowed me to develop a greater appreciation of the complexity of the social-ecological dilemma that this thesis confronts. These insights inspired Chapter 5, in which the application of widespread *ribeirinho* viewpoints to a social science vulnerability framework allowed me to better understand and voice their concerns, while contributing to the poorly studied concept of social-ecological feedbacks. Overall, this thesis provides unique evidence of the extent of rainforest city-driven defaunation, establishes novel empirical links between wildlife catch rates and food insecurity, and between food insecurity and bushmeat offtake, while advancing conceptual understanding of the two-way connection between human and ecological vulnerability. This evidence furthers current understanding of the predicament of sustainable wild animal protein production in the Amazon. Although my new evidence presents a pessimistic view of the extent of the issue for Amazonian ecosystems and people, I optimistically discuss ongoing and potential future changes in the approach to conservation in the Amazon, which increasingly strives to incorporate people. It is my belief that the concepts and methods applied in this research are highly applicable to other wild food systems worldwide.

6.1.1. Amazonia's urbanised wilderness

Amazonia has been described as an urbanised wilderness (Padoch *et al.* 2008; Parry, Barlow & Pereira 2014), as within just 60 years the proportion of the urban population has shifted from a quarter to three quarters (IBGE 2010a). Urban areas in Amazonia are also having a significant influence on rural people, with improved transport connections, and a greater two-way exchange of goods and services (Padoch *et al.* 2008). Through analysing harvesting profiles, I show that distance to Manaus, the Amazon's largest city, dictates which species of fish *ribeirinhos* catch (Chapter 4). The mechanism I have proposed for this is the presence of a regular ferry/cargo boat service that purchases fish and deposits ice, but only in communities closer to Manaus. This mechanism appears to also explain the defaunation of Manaus' favourite fish species, the tambaqui (*Colossoma macropomum*), which is smaller (mean body size) and harder to catch (catch-per-unit-effort by biomass; CPUEb) within the range of this boat service (Chapter 2). Moreover, I show that tambaqui populations appear to be depleted up to 1000 km from Manaus. I discuss how the important roles of tambaqui, both as a seed disperser in the flooded forest and as an income generator, may be threatened.

Despite detecting a spatial gradient of overfishing-driven defaunation (Chapter 2), it is interesting that I detected no such gradient in fish catch rates (CPUEb) or food insecurity (Chapter 3). This could be explained by biological or harvester behavioural compensatory changes, which result in a very different species catch profile in remote areas (Chapter 4). My data shows a local reliance on fish (Chapter 3), while domestic meat (chicken and beef) consumption was rare, which implies that it is of lower importance to food security than has been suggested elsewhere in the literature (Nardoto *et al.* 2011; van Vliet *et al.* 2015a; de Jesus Silva *et al.* 2016). However, I found that the frequency of domestic meat consumption is much greater nearer to urban areas relative to more remote areas.

6.1.2. The seasonally flooded forest

Water levels in the Amazon basin naturally fluctuate by as much as 15m, inundating vast tracts of forest for around half the year. *Ribeirinhos* are well adapted to these hydrological changes (Harris 1998), but what have been considered "once in a century" floods and droughts are now occurring regularly and at a greater intensity (Marengo *et al.* 2013). The seasonally increased volume of water reduces fish concentrations (Saint-Paul, Zuanon & Correa 2000; Pinho, Marengo & Smith 2015), and I show that this makes them much harder to catch (lower CPUEb), which coincides with a fall in household fish catch biomass (Chapter 3). *Ribeirinhos* appear to attempt to compensate for reduced fish catch by spending longer fishing and hunting, but not by increasing domestic meat consumption. Importantly, bushmeat hunting offtake from forests increases significantly during this lean high-water season. Despite their efforts to adapt, I show that *ribeirinhos* suffer from severe food insecurity during this period (Chapter 3), and in doing so I draw novel empirical links between wildlife catch rates and food security.

6.1.3. Vulnerability of the Amazonian floodplain social-ecological system

Conservation problems are rarely confined to disciplinary (social and natural) or environmental realm (marine, freshwater and terrestrial) boundaries, and hence conservation research and management is increasingly striving to cross them (Rowcliffe, Milner-Gulland & Cowlishaw 2005; Castree *et al.* 2014). I see this interdisciplinary approach as essential for understanding the linkages among biodiversity conservation, rural livelihoods and food security in Amazonia and elsewhere. Some of the most important contributions of this thesis are made by identifying novel empirical links between food insecurity and ecology. For example, I provide original evidence that rural harvesters are highly vulnerable to changes in the relative abundance of fish (Chapter 3), and that their vulnerability appears to drive increased hunting pressure on terrestrial species (Chapter 4). In feeling that I needed to voice the widely expressed views of local fishers, I found myself, an ecologist by training, delving further into the social science literature. I eventually decided that 'vulnerability' was the best conceptual approach to frame what I viewed to be some of the key concerns of *ribeirinhos*. In exploring this framework in more detail I realised that an important part of my quantitative and qualitative findings fits well into a knowledge gap concerning poorly understood social-ecological feedbacks. Urban-driven defaunation (Cinner *et al.* 2016), wildlife-catch determined food insecurity (Golden 2016), fish-bushmeat substitutions (Endo, Peres & Haugaasen 2016) and social-ecological feedbacks (Larrosa, Carrasco & Milner-Gulland 2016) are all at the forefront of interdisciplinary conservation science. The identification of severe food insecurity among *ribeirinhos* permitted me to make some novel connections between these areas, framed in the context of evidenced vulnerability.

6.1.4. Wider application

While my work is clearly most relevant to conservation and development in the Brazilian Amazon, I believe that each chapter makes important contributions to our understanding of the dynamics of wildlife harvest systems globally. Chapter 2 demonstrates long distance urban-driven defaunation extending deep into remote tropical forests. These results offer stark warnings to tropical Africa and Asia where urban wildlife consumption is significant, and where urbanisation and economic development is behind the Brazilian Amazon, but catching up. For example, while the proportion of Brazil's population living in urban areas has risen by 4.5% since 2000, in the Democratic Republic of Congo and Indonesia (the other main tropical rainforest host nations) it has risen by 7.4% and 11.7% respectively (UN 2015).

In Chapter 3 I identify severe seasonal food insecurity among rural Amazonians, providing evidence that wildlife catch rate can determine food security. This evidence implies that wildlife-dependent human populations worldwide are vulnerable to drops in the relative or absolute abundance of wildlife, which could be driven by such stresses as climate change driven hydrological changes or overexploitation. On the other hand, I also warn against overstating food security impacts of overharvesting, because fish catch rates and food security levels appeared stable (Chapter 3) along a spatial gradient of defaunation (Chapter 2). My correlative evidence suggests there are causative links between seasonal food insecurity and increased bushmeat offtake in Chapter 4. This furthers global evidence that low fish availability can result in greater hunting pressure (Brashares *et al.* 2004; Endo, Peres & Haugaasen 2016), and is first empirical evidence that hunting may be an arguably necessary adaptive response to harm. Framing this evidence within the context of social-ecological feedbacks within Chapter 5, I hope to stimulate greater consideration of human natural resource user vulnerability in conservation research and management, and the critical importance of holistic and adaptive thinking in complex social-ecological systems (Castree *et al.* 2014).

6.2. Future research

6.2.1. The value of different species for nutrition and livelihoods

The vulnerability of wildlife-reliant people to food and livelihood insecurity is a major theme of this thesis. In addition to evidence that people may be at risk when wildlife availability and access is restricted (Chapter 3), we discuss the importance of recognising that the nutritional and financial value of certain species varies (Chapter 2, Chapter 4). Thus, seasonally fat-rich frugivorous fish may have a disproportionately high importance for food insecure people during the lean high water season (Chapter 3, Chapter 4). Moreover, some large preferred fish species are particularly profitable (Chapter 2), and others that have an established market in being sold salted may be essential in areas with poor access to refrigeration

(Chapter 4). Hence, I have argued that in some cases wild-meat biomass is an oversimplification of nutritional and livelihood issues.

I believe that a greater understanding of the nutritional needs of rural people and the nutritional values of different species is required (Cawthorn & Hoffman 2015). For example, to what extent is the overwhelming preference of *ribeirinhos* for threatened tambaqui (Chapter 2) a product of 'deliciousness' alone, and to what extent does it represent a rare and essential source of fat in a potentially seasonally fat-limited population? I think conservation scientists and practitioners need to better consider the social implications of reduced availability and access to nutritionally and financially important species, which can be caused by their defaunation or environmental restrictions.

6.2.2. Social-ecological feedbacks

Social-ecological feedbacks are another neglected area of research, the poor understanding of which could potentially undermine much academic and practical conservation work (Larrosa, Carrasco & Milner-Gulland 2016). In Chapter 5 I combine findings from the literature (Brashares *et al.* 2004; Endo, Peres & Haugaasen 2016) and my own research findings (Chapter 4) that fishers increase hunting pressure on terrestrial wildlife when fishing becomes difficult. Perspectives from local people in the Amazon floodplain imply that legislative efforts to conserve charismatic pink river dolphins (*Nia geoffrensis*) may indirectly cause harm to other sensitive wildlife populations such as turtles (mainly *Podocnemis expansa* and *Podocnemis unifilis*). However, our understanding of the prevalence of such legislative-driven feedbacks remains limited by the anecdotal nature of the evidence, and decision-making cannot rely on anecdotal evidence and conceptual frameworks alone (Larrosa, Carrasco & Milner-Gulland 2016).

I believe that further research into the potential harvester-switching behaviour following restrictions on key natural resources is needed. While such work would need to be carefully designed, I think that we could learn a lot from interviews that aim to document changes in harvesting practices with those people whose principal livelihood activities have recently been banned. Efforts to protect vulnerable species from overexploitation are important, although it would be short-sighted to assume that preventing wildlife-dependent people from harvesting certain specific taxa will be without its disadvantages. Resource harvesters with few options for formal employment yet a breadth of skills and local ecological knowledge have major incentives to innovate in order to gain income and feed their families.

6.2.3. Holistic research of social-ecological systems

Lastly, to what extent do any of my conclusions matter for management and policy if human behaviour and market forces will compensate for over-harvesting of particular species? Will defaunation of commercially-important wildlife merely increase their value, and/or the value of once-unimportant species? If tambaqui went extinct in the wild, would Manaus just find a new favourite fish species for *ribeirinhos* to target (e.g. Pauly *et al.* 1998), or would a compensatory expansion of farmed tambaqui and/or domestic meat end the market for *ribeirinho*-caught fish via expensive long-distance transport? Given that spatial trends in fish defaunation (Chapter 2) were not matched with CPUEb and food insecurity trends (Chapter 3), will *ribeirinhos* be able to maintain nutritious diets by 'fishing down' the price list? Might constraints on fishing as a livelihood contribute to a rural exodus, and could this actually be beneficial for human-wellbeing, or would *ribeirinhos* just end up in urban slums (Neto, Torres & de Almeida 2014)? Although I have tried to take a holistic view in this thesis, the potential environmental and social changes and feedbacks are far too many and complex to predict. However, I believe that only through a holistic vision (appreciating the inherently linked basis of social-ecological systems and accounting for aquatic-terrestrial interactions) and an adaptive approach to management, will we be able to meet the demand for animal protein at the lowest cost to Amazonian ecosystems.

6.3. Concluding remarks

This thesis exemplifies the complexities central to social-ecological systems, and the challenges of sustainably feeding a changing population in a modern tropical rainforest system. In exploring the biodiversity conservation and food security dimensions of rural livelihoods and resource harvesting, I show that their activities, diet and the condition of their natural resource base are strongly determined by hydrological seasons and urban market forces. I demonstrate the great extent to which Amazonian people both strongly impact and depend on Amazonian ecosystems, by revealing urban market driven defaunation deep into rainforest wilderness, and severe food insecurity resulting from drops in fish relative abundance. My results also provide a warning due to declines in certain financially and nutritionally valuable species in situations where local people are particularly vulnerable. Finally, I integrate the perspectives of local resource-users into my research, and show how human vulnerability to environmental and legislative stresses may result in ecological harm as local people try to adapt by switching harvesting pressure to other sensitive taxa. With these findings, I provide novel insights and perspectives into the complex linkages between human, freshwater and terrestrial components of the Amazon social-ecological system. I conclude that successfully achieving sustainable and sufficient food production in the Amazon and other harvesting systems must consider such linkages by taking a holistic and adaptive view to research and management.

6.4. References

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