Wildlife responses to anthropogenic disturbance in Amazonian forests

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Abstract

Legally inhabited indigenous, extractive and sustainable use tropical forest reserves, have been lauded as a solution to the intractable problem of how to assure the welfare and secure livelihoods of the world's diverse forest-dependent people, whilst conserving the world's most biodiverse terrestrial ecosystems. This strategy has been critiqued by human rights advocates, who assert that legally inhabited reserves paternalistically restrict the livelihood choices and development aspirations of forest-dwellers, and by conservationists, who argue that sustained human presence and resource extraction erodes tropical forest biodiversity. This thesis examines both the anthropogenic impacts on tropical forests at the regional, landscape and household scales and the livelihood challenges faced by semi-subsistence local communities in the Brazilian Amazon. A spatially explicit dataset of 633,721 rural Amazonian households and an array of anthropogenic and environmental variables were used to examine the extent and distribution of structural (deforestation) and non-structural (hunting) human disturbance adjacent to 45 cul-de-sac rivers across the Brazilian states of Amazonas and Pará. At the landscape and household scales, a total of 383 camera trap deployments, 157 quantitative interviews and 164 GPS deployments were made in the agricultural mosaics and forest areas controlled by 63 semi-subsistence communities in the Médio Juruá and Uatumã regions of Central-Western Brazilian Amazonia, in order to quantify and explicate the (i) livelihood costs incurred through the raiding of staple crops by terrestrial forest vertebrates, (ii) degree of depletion that communities exert upon the assemblage of forest vertebrates and (iii) spatial behaviour of hunting dogs and their masters during simulated hunts. Our results indicate that at the regional scale, accessibility, fluvial or otherwise, modulated the drivers, spatial distribution and amount of anthropogenic forest disturbance. Rural household density was highest in the most accessible portions of rivers and adjacent to rivers close to large urban centres. Unlike the low unipolar disturbance evident adjacent to roadless rivers, road-intersected rivers exhibited higher disturbance at multiple loci. At the household and landscape scales semi-subsistence agriculturalists lost 5.5% of their staple crop annually to crop raiders and invested significant resources in lethal and non-lethal strategies to suppress crop raiders, and to avoid losses an order of magnitude higher. Crop raiding was heightened in sparsely settled areas, compounding the economic hardship faced by communities already disadvantaged by isolation from urban centres. A select few harvest-sensitive species were either repelled or depleted by human communities. Diurnal species were detected relatively less frequently in disturbed areas close to communities, but individual species did not shift their activity patterns. Aggregate species biomass was depressed near urban areas rather than communities. Depletion was predicated upon species traits, with large-bodied large-group-living species the worst impacted. Hunting dogs travelled only ~ 13% farther than their masters. Urban hunters travel significantly farther than rural hunters. Hunting dogs were recognised to have deleterious impacts on wildlife, but were commonly used to defend against crop raiders.

Chapter 1: Introduction

1.1 Tropical forests; importance and threats

Tropical forests have stood for some 60 million years, and harbour the majority of the Earth's ~6.5 million terrestrial species (Burnham and Johnson, 2004, Mora *et al*., 2011). Yet since the mid-1900s, roughly half of all tropical forests globally have been felled by a single species (Fagan *et al*., 2006). Anthropogenic threats are simultaneously eroding tropical biodiversity and the natural capital on which humanity depends. Apart from the immeasurable existence value of tropical forests, they also provide a wealth of poorly quantified ecosystem services, maintaining a biosphere amenable to human existence. These services include carbon storage, climate regulation, water purification, and a source of novel pharmaceutical chemicals, which are crucial to humanity in general (Costanza *et al*., 1997). They also provide habitat for timber and non-timber forest resource populations, and a multi-billion dollar trade in wild-caught fish and meat which underpins the livelihoods and subsistence of forest dwellers, who are some of the world's poorest people (Clay and Clement, 1993; Robinson and Bennett, 2013).

Tropical forests are also simultaneously threatened with deforestation, degradation and defaunation. Deforestation is fuelled by population growth, colonisation and shifting global consumption patterns (Allen and Barnes, 1985; McAlpine, *et al*., 2009; Schneider and Peres, 2015), enabled by road-building (Kirby *et al*., 2006; Adeney *et al*., 2009) and driven largely by mechanized agricultural expansion (Brady, 1996; Tilman *et al*., 2001; Gibbs, *et al*., 2010), especially for the production of beef, soy and palm oil (Fitzherbert., *et al* 2008; Nepstad *et al*., 2014). Forest degradation results from wildfires, fragmentation, logging, livestock grazing and biomass removal, especially for fuelwood and for charcoal production (Laurance *et al*., 2002, Matricardi *et al*., 2010; Hosonuma *et al*., 2012). Lastly, anthropogenic climate change is predicted to result in much dryer conditions in seasonally-dry tropical forests including a large portion of the Amazon, exacerbating the aforementioned threats and potentially resulting in large-scale habitat shifts towards lower biomass and lower diversity ecosystems (Malhi *et al*., 2009).

It is estimated that over 5 million tonnes of wild mammal meat is extracted annually from Neotropical and Afrotropical forests alone (Fa and Peres, 2001). The removal of forest vertebrates by hunters has been dubbed a "bushmeat crisis", responsible for creating "empty forests" in which species larger than 2kg are virtually absent (Redford, 1992; Bennett *et al*., 2002; Harrison, 2011). Though commercial hunters are often implicated in wildlife declines (Bowen-Jones and Pendry, 1999), local populations of harvest sensitive species may be severely depressed even by isolated households of subsistence hunters (Peres, 1990). Overhunting poses both a direct threat to the targeted species and an indirect threat to the forest as a whole. Larger-bodied, slow-reproducing species, such as primates are especially vulnerable to overhunting (Ripple *et al*. in press). The removal of large-bodied species that previously acted as ecosystem engineers and seed dispersers (Desbiez and Kluyber, 2013; Peres *et al*., 2016), has far-reaching, long-term consequences, deflecting some trajectories of forest regeneration more typical of faunally-intact forests (Wilkie *et al*., 2011).

The impacts and even the nature of subsistence hunting in tropical forests are the subject of divisive academic debate. Subsistence hunters are typically central place foragers, whose hunting effort is concentrated in the first few kilometres from the household (Alvard *et al*., 1997). Some argue that they behave as optimal foragers, always pursuing profitable prey regardless of prey species vulnerability and adopting the most efficient technologies available to them, resulting in the depletion, repulsion and extirpation of vulnerable species in multi-prey assemblages (Hawkes *et al*., 1982; Mittermeier, 1987; Branch *et al*., 2013). Others argue that subsistence (especially traditional) hunters have a well-developed conservation ethic, and that their selective resource and spatial utilisation rules result in a sustainable harvest of game species (Read *et al*., 2010; Vliet *et al*., 2010).

1.2 Social context

Nation states with sovereignty over the world's remaining tropical forests are generally monetarily poor and have rapidly growing and increasingly market-integrated populations (Cincotta *et al*., 2000; Sachs *et al*., 2001). Such populations require both agricultural land and forest timber and non-timber forest products. The effects of population growth are multiplied by the increase in per capita consumption, which is in part a desirable consequence of declining poverty, but also a cultural phenomenon resulting from the emulation of the unsustainable consumerism characteristic of "developed" nations (Wilk, 1998).

Globally, and especially in tropical nations, populations have urbanised rapidly in the past century (Cohen, 2006). This process is a mixed blessing for tropical forest conservation. By reducing the population density in rural areas, urbanisation potentially reduces the direct pressures of both the extraction of wild meat and agricultural clearing, and may lead to land abandonment and forest regrowth (Cramer *et al*., 2008; Fearnside, 2008). Wealthier urbanites however, have a higher disposable income and higher per capita consumption than their rural counterparts (Margulis, S., 2004). Though direct pressure is thus reduced, the net pressure, including displaced resource-use by urbanites, has increased. Furthermore, the local power vacuum left behind by a depopulated countryside may render forests more vulnerable to large-scale disturbance including timber extraction, commercial hunting (Parry *et al.*, 2010), goldmining and petroleum extraction.

National governments and the international community have both ameliorated and exacerbated the threats faced by tropical forests. Encouraged in part by the commitments made in the Convention on Biological Diversity (CBD), nation states have legally protected over 13% of the Earth's surface (Venter *et al*., 2014) including 19% of the Earth's tropical humid forest (Chape *et al*., 2005). Likewise, the Convention on International Trade in Endangered Species (CITES), has placed legal restrictions on the international trade of threatened species including mahogany

(Verissimo *et al*., 1995). Lastly, finance mechanisms including the Reducing Emissions from Deforestation and Forest Degradation (REDD) and other Payments for Ecosystem Services (PES) schemes including the Brazilian Bolsa Floresta, aim to harness global capital to finance the protection of forests and their carbon in developing nations.

These measures have not been without controversy and criticism however. Efforts by the international community to instigate strictly protected areas in tropical countries have been branded "conservation imperialism" and "fortress conservation" (Guha, 2003; Siurua, 2006). They are deemed hypocritical measures imposed by nations that have already enriched themselves through wholescale ecological destruction, which threatened or devastated the livelihoods of aborigine communities and involve grievous human rights abuses (Hutton *et al*., 2005). REDD has been sharply critiqued, not only for its flawed methodology (Clements, 2010; Watch, 2013), but because it is perceived to be an effort to simultaneously permit wealthy polluters to continue "business as usual", whilst disenfranchising the rural poor (Griffiths and Martone, 2008). National governments are likewise criticised for investing tax revenues in mega-projects with disastrous environmental and social consequences (Fearnside 1989), promoting the exodus of neocolonists to tropical forest areas (Peres and Schneider, 2012), providing perverse financial incentives for deforestation (Binswanger, 1991), and engaging in rest seeking behaviour whilst colluding with illegal loggers (Palmer, 2001)

1.3 The Brazilian Amazon and its inhabitants

Though tropical regions are ecologically and socially distinct, the Brazilian Amazon exemplifies many of the aforementioned themes. The Amazon is the largest contiguous tropical forest on Earth, harbouring a quarter of global terrestrial biodiversity (Malhi *et al*., 2009) but experiences the globally highest levels of absolute deforestation (≈2 Mha yr^{-1}, Laurance *et al*., 1998). Roughly 44% of Brazilian Amazonia falls under nonprivate conservation areas, 80.4% of the area of which is allocated to legally inhabited reserves in which residents may pursue extractive livelihoods (Peres, 2011)

The Brazilian Amazon is inhabited by ~25M people of diverse socio-ethnic backgrounds. Populations are divided between sparsely inhabited hinterlands and dense cities and such as ~2M strong Manaus, which encompasses over half of the inhabitants of the ~1.6M km2 state of Amazonas. Amazonian urban and rural domains are however intertwined. The vast majority of urbanites are recent migrants. Many were either born in rural communities, or still have extended family there. As a result, rural-urban networks are maintained and multi-sited households are common (Pinedo-Vásquez and Padoch, 2009). Many households attempt to benefit from both the access to goods and services afforded by a town and the access to natural resources afforded by the hinterland. These households often garner resentment from their fellow community members, who consider their appropriation of land, fish and other natural resources to be excessive and unwarranted.

Rural Amazonians include over 300,000 Indigenous Amerindians belonging to around 160 diverse linguistic and cultural groups, 50 of which are amongst the last remaining uncontacted tribal groups on Earth (Cunha and De Almeida, 2000). The pre-Columbian Amazonian population density is a matter of scholarly debate, but the presence of Amazonian dark earth (*terra preta*. Lima et al., 2002), an anthropogenic soil created over long periods of charcoal enrichment, indicates that in favourable locations including river bluffs and areas of fertile floodplain (Denevan, 1996), populations were dense and longstanding. Europeans decimated the population of Amerindians through both deliberate extermination and the introduction of novel diseases (Roosevelt, 1997). Amerindians are still subject to deep-seated prejudice in Brazilian society, part of which views then as an uncivilised obstacle to progress (Pallemaerts, 1986).

According to the Brazilian Institute of Geography and Statistics (IBGE) 97% of the population of Amazonia do not identify themselves as indigenous. In the last three decades, new waves of colonists have arrived in the Amazon from central-southern Brazil, enticed by government subsidies and Instituto Nacional de Colonização e Reforma Agrária (INCRA) resettlement programs (Binswanger, 1991). The majority of rural Amazonians are neither newly arrived colonists, nor indigenous Amerindians however, but mixed heritage river dwellers (*ribeirinhos*), who are the main focus of this study.

As their name suggests, *ribeirinhos* have settled along Amazonian waterways. Many did so in search of rubber during the rubber boom of 1890-1930. These *seringueiros* (rubber tappers) became the debt-slaves of wealthy rubber barons (*patroes*) who claimed monopolistic control of river basins and extracted a rubber tithe, whilst simultaneously controlling access to goods and services (Hvalkof, 2000). The early biopiracy of the British broke the Brazilian rubber monopoly by creating plantations in SE Asia, which ultimately caused the crash of the Brazilian rubber industry (Brockway, 1979). The majority of *seringueiros* migrated to cities during the collapse of the rubber industry beginning in the early 1900s (Resor, 1977) but the remainder still engage in semi-subsistence agricultural and extractive livelihoods. Freedom from *patroes* did not necessarily entail prosperity. High transport costs meant that rural *ribeirinhos* have been prey to *regatoes*, river-based merchants with a virtual monopoly on trade, who exchange manufactured goods directly for agricultural produce at an unavoidably high price (Cleary, 1993). The increased availability of small outboard motors (*rabetas*), the regional reduction in the trade of animal pelts and skins (Bodmer *et al*., 1988) and the creation of producer cooperatives for farinha and rubber within the past few decades have greatly diminished the influence of *regatoes*. During the 1970s, *seringueiros* whose livelihoods depended on extracting resources from standing forests stood in the way of land-seeking cattle-ranchers. The murder of human rights leader and extractive union campaigner Chico Mendes, galvanised the movement to instate extractive and sustainable use reserves to legally protect the livelihoods of extractivists and the forests on which they depend (Fig. 1.1). Consequently, ~ 63.1 million ha of sustainable-use reserves were created in Brazilian Amazonia since 1991 (Peres, 2011).

***Figure 1.1**. Examples of Amazonian extractive livelihood activities including the harvest and processing of* Euterpe oleracea *(locally* açaí*) (A & D), fishing (B), extraction of latex rubber from a rubber tree (*Hevea brasiliensis*) (C) basket weaving using* Heteropsis flexuosa *(locally* cipó titica*) (E), extracting sawn timber (F) and a hunted* Cuniculus paca *(locally* paca*) (G) (Photos: MIA)*

Amazonian forests are also highly heterogeneous given their baseline geomorphological and edaphic templates (Fig. 1.2). River basins can be classified into three types based on the chemical properties of the river. Rivers that drain from the geologically young Andes are termed “white-water” rivers (Sioli, 1950). They are virtually pH neutral and carry a heavy sediment load and consequently enrich the white-water *várzea* floodplains during the seasonal flood pulse (Junk *et al*., 1989). Rivers draining from basins dominated by sandy soils, are acidic and tannic from partially decayed dissolved plant matter and are termed “black-water” rivers. They are bordered by *igapó* forests and nutrient-poor dwarfed wooded vegetation such as *campina* and *campinarana*. Lastly, low sediment “clear-water” rivers mostly drain from the Brazilian and Guianan shields. River chemistry has a powerful impact on human livelihoods. Black-water rivers have been called “hunger rivers” by their inhabitants due to nutrient-poor soils and scarcity of wild protein sources (Janzen, 1974), though the acidic waters suppress disease vectors including mosquitos and sandflies.

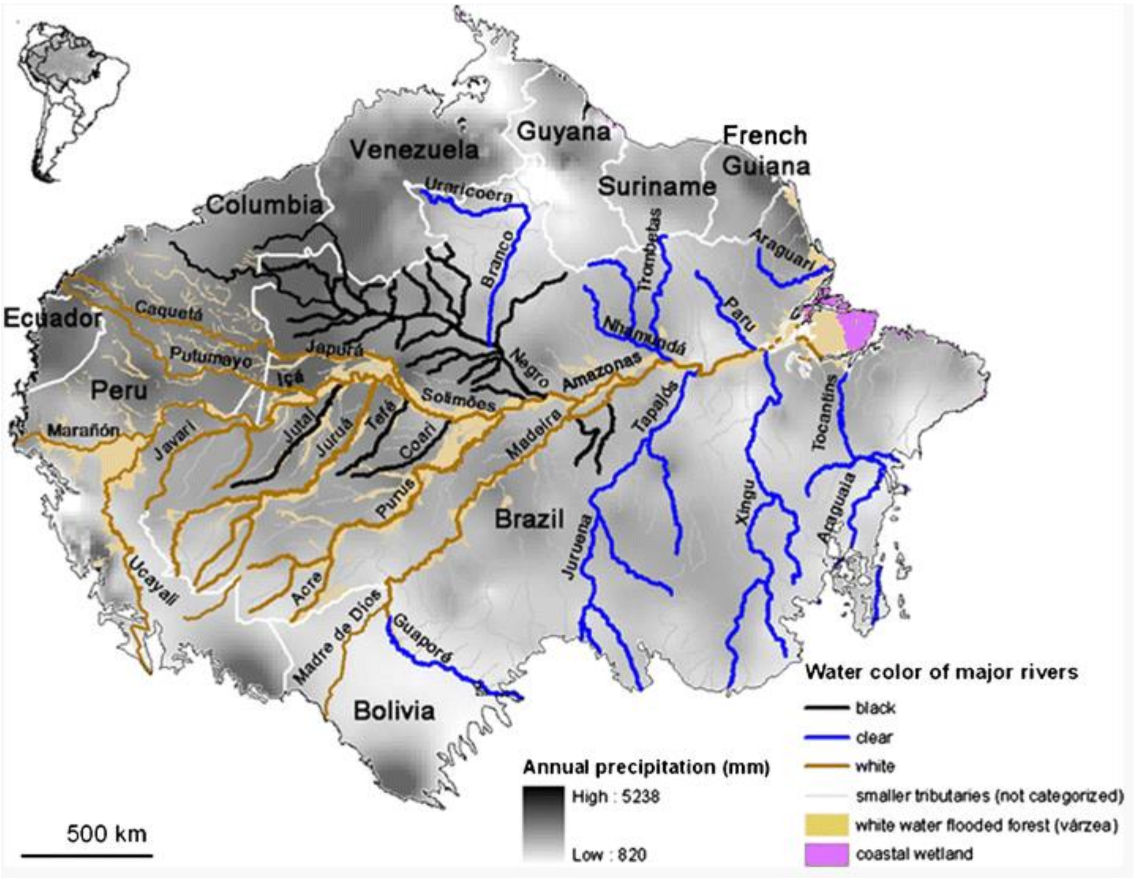

Figure 1.2*. The distribution of major whitewater, blackwater, and clearwater rivers in the Amazon basin.* Source: Junk, *et al*., 2011

1.4 The Médio Juruá and Uatumã study regions

The bulk of this thesis focusses upon the Médio Juruá and Uatumã regions of Western and Central Brazilian Amazonia, respectively, which are centred around three extractive and sustainable use reserves. The Médio Juruá study region covers an area of 1,637,008 ha and consists of 63.9% of primary unflooded (*terra firme*) forest, 30.0% of seasonally-flooded *várzea* forest, 4.4% of permanent water bodies, which include the Juruá River (the second-largest white-water tributary of the Amazon) and its tributaries and oxbow lakes, and 1.8% deforestation. Two sustainable-use reserve - the Uacari Sustainable Development Reserve and the Médio Juruá Extractive Reserve - jointly protect 42.3% of this landscape. The nearest towns are Carauari, which is 88 fluvial km downriver from the Médio Juruá Reserve and has a population of 4145 families, and Itamarati, which is 120 fluvial km upstream from the Uacari Reserve and has a population of 905 families.

The Uatumã study region covers an area of 1,601,704 ha and consists of 62.3% of undulating upland primary unflooded (*terra firme*) forest, 17.9% of primary low-lying and seasonally-flooded *igapo* forest, 11.1% permanent water bodies, which include the Uatumã River (which connects the Balbina reservoir to the Amazon River) and its main tributary the Jatapú River, 4.0% deforestation and 4.7% of *campina* and *campinarana* non-forest vegetation on oligotrophic soils. The Uatumã Sustainable Development Reserve legally protects 27.0% of this landscape. The nearest towns are Vila Balbina, which has a population of 420 families and is 66 fluvial km upstream of the reserve, and Sao Sebastião, Itapiranga and Urucará, with populations of 1214, 1345 and 2051 families, respectively, and are 37, 40, and 53 fluvial km downriver of the reserve, respectively.

Both regions are inhabited by *ribeirinhos*, with producer cooperatives and resource-management programs. Large-scale ecological and socioeconomic differences between the two study regions are due to river chemistry and proximity to Manaus, the largest city in Brazilian Amazonia. The Juruá region encompasses white-water floodplain ecosystems, whereas the Uatumã region encompasses black-water ecosystems. Secondly, the Juruá region is over five times farther from Manaus, which increases transaction costs and reduces market opportunities for Juruá inhabitants.

Manioc (*Manihot esculenta*) is the staple source of carbohydrates in our study regions, as in much of the humid tropics (Cock, 1982; Frazer, 2010). Crops including maize and bananas are also locally important, but their higher nutrient requirements prevent their large scale cultivation in most of Amazonia. The main varieties of manioc are high-cyanide manioc (Peroni *et al*., 2007), locally called “*roça brava*”, and low-cyanide manioc, locally called “*macaxeira*”. *M. esculenta* produces large tubers, tolerates poor tropical soils and is pest-resistant. Manioc is processed in a flour-house (locally “*casa de farinha*”) into a relatively imperishable, high calorie course flour (locally “*farinha*”) (Fig. 1.3). Communities grow manioc in swidden agricultural plots called *roçados*, often representing the main livelihood activity for semi-subsistence riparian communities in the lowland Amazon (Newton *et al*., 2012). *Roçados* are generally active for 4 years until weed encroachment and declining soil fertility force their abandonment (Unruh, 1988). The resulting secondary forests (locally "*capoeiras*") are then left to undergo successional regrowth until standing biomass and soil nutrient loads are sufficient to permit re-clearing. This shifting agriculture process creates a mosaic of habitats under different successional stages around village settlements, with shorter-rotation plots generally closer to the community (Coomes *et al*., 2000).

***Figure 1.3**. The cultivation and processing of manioc (*Manihot esculenta*). A cleared and burned agricultural plot (*roçado*) with immature manioc plants (A) and maturing manioc plants (B). The peeling (C), grinding, sieving and roasting (D) of manioc into* farinha. *(Photos: MIA)*

1.5 The challenge of sustainable use

Amazonian sustainable use and extractive reserves were created with the dual purpose of maintaining human extractive livelihoods, as well as protecting the biodiverse forest ecosystems upon which those livelihoods depend. Many conservationists consider these dual aims to be in conflict. They argue that human occupation of protected areas inevitably results in habitat degradation and species extirpation and that biodiversity is best served through the enforcement of strictly protected areas (Kramer *et al*., 1997, Brandon *et al*., 1998).

Figure 1.4. *Examples of natural resource management programs in the Juruá region. The monitoring of river turtle (*Podocnemis spp.*) nesting beaches (A) and the offtake of pirarucu (*Arapaima gigas*) from managed oxbow lakes (B). (Photos: MIA)*

Many tropical forest resources, including timber and wild-caught game animals and fish are classic examples of common pool resources (Ostrom, 2005) in that they are both rivalrous and non-excludable. This makes them especially vulnerable to a ‘tragedy of the commons’, in which all users are incentivised to extract as much as possible, leading to stock collapses. Such collapses are indeed evident in stocks of timber and of certain large-bodied species of fish regionally (Castello et al., 2011; Richardson and Peres, 2016) and locally for populations of Brazilian Rosewood (*pau rosa*) in the Uatumã region and of pirarucú (*Arapaima gigas*) and river turtles (*Podocnemis* spp.) in the Juruá region (but see Campos-Silva & Peres 2016). Recent community resource management programs for pirarucu in the Juruá region have however proven effective at restoring fish stock (Silva, 2014). Pirarucú, congregate in oxbow lakes, seasonally detached from the main river during the low water season, and occasionally surface to breathe. This facilitates both their monitoring and the exclusion of non-residents (Fig. 1.4). In addition, the Bolsa Floresta program, managed by the Fundação Amazonas Sustentável (FAS) is a payments for ecosystem services (PES) scheme that incentivises communities to avoid deforesting primary forest and to implement timber stock management strategies (Vianna and Fearnside, 2014).

The management of subsistence hunting has however proven a greater challenge. Many of the large and highly prised game species such as South American tapir, are far less productive than even large aquatic species, such that their populations are likely to respond more slowly to offtake management. Furthermore, populations of terrestrial game species are difficult to locally monitor (Munari *et al*., 2011, Constantino *et al*., 2012) and excluding hunters from the forests they inhabit is virtually impossible. As part of a government-funded resource management program (Programa de Monitoramento da Biodiversidade e do Uso de Recursos Naturais em Unidades de Conservação Estaduais do Amazonas, ProBUC) and the Projeto Médio Juruá (led by Prof CA Peres, University of East Anglia), line transect surveys have been conducted in both the Juruá and Uatumã regions as a means of faunal monitoring. As a means of monitoring hunted populations, line-transects surveys have however been criticised for their detectability biases, because hunted species are known to change their behaviour in response to persistent hunting and other anthropogenic disturbance, such that they become less detectable (Johns, 1985). Though the use of camera trapping rates to infer relative abundance is not without problems (Sollmann *et al*., 2013), camera traps are becoming ubiquitous tools in conservation and ecology (Rowcliffe and Carbone, 2008) and they potentially offer a monitoring solution that circumvents species behavioural responses to human surveyors.

1.6 Aims and thesis structure

The overarching aim of this study on wildlife responses to anthropogenic disturbance in Amazonian forests, was to examine the degree to which current human occupation and extractive use of tropical forests is compatible with biodiversity conservation. To that end, research was carried out at the regional, landscape and community scales, and encompassed both the ecological/biotic impacts of human activities, and the conflicts generated by human livelihoods and extractive practices. This study was developed in response to the threats to tropical forests identified above, and the potential for legally inhabited sustainable use and extractive reserves to serve dual social and conservation purposes.

The four data chapters of this thesis were written in manuscript format, with the intention of publishing each separately as articles in peer-reviewed journals. As such, each chapter contains its own reference list and appendices and some repetition is unavoidable in material within the methods sections.

Chapter 2: A regional-scale approach and Geographic Information System (GIS) tools were used to quantify and compare patterns of structural and non-structural anthropogenic disturbance across 45 cul-de-sac roadless and road-intersected navigable rivers throughout the states of Amazonas and Pará. Whole-river and fluvial-segment analyses were employed to elucidate within-river and between-river patterns. The relative importance of environmental, local and non-local anthropogenic factors in driving forest disturbance, was discussed.

Chapter 3: The prevalence and livelihood impacts of terrestrial vertebrate crop-raiding damage to manioc semi-subsistence agricultural plots in the Médio-Juruá region was quantified, contextualized and explained using camera traps and structured interviews. The degree to which subsistence hunting gains are sufficient to offset losses to crop raiders, as well as the complementarity of social and ecological research approaches, were discussed.

Chapter 4: Camera traps and structured interviews were used to survey the peri-community areas controlled by semi-subsistence communities in both the Médio Juruá and Uatumã regions, in order to quantify envelopes of depletion of forest vertebrates in proximity to human communities. The anthropogenic impacts on the detection rates of individual species, the aggregate biomass of forest vertebrates and on faunal activity patterns, at both the community and landscape scale, were assessed. The extent to which community-based subsistence offtake is compatible with ecologically functional populations of tropical forest game species, was discussed.

Chapter 5: The spatial behaviour of hunting dogs and their masters during simulated hunts in the Juruá and Uatumã regions, was characterised. The effectiveness of novel GPS units was compared to that of commercially available alternatives. The ecological costs and social benefits of the use of hunting dogs, were discussed.

Chapter 6: The main findings of the four data chapters were summarised. Themes common to the four data chapters were synthesised and discussed. Lastly, potential conservation strategies and fruitful areas of future research were indicated.

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Chapter 2: External determinants of structural and non-structural forest disturbance along Amazonian cul-de-sac rivers

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Abstract

Infrastructure development in the Brazilian Amazon continues apace, opening new frontiers into hitherto remote, previously undisturbed areas, yet the spatial extent of different patterns of human-induced structural (deforestation) and non-structural (hunting) disturbance in tropical forest regions is yet to be investigated simultaneously. This study examines an aggregate area of 301,641 km² adjacent to 45 cul-de-sac rivers across the Brazilian states of Amazonas and Pará. These rivers represent the interface between highly accessible fluvial highways and remote forest headwaters across Amazonia, which are becoming integrated to varying degrees into an expanding network of roads and towns, eroding their inaccessibility. We use a spatially explicit dataset of 633,721 rural Amazonian households and an array of anthropogenic and environmental variables to firstly quantify and compare patterns of structural and non-structural anthropogenic disturbance, and to secondly examine correlates of deforestation such as rural population density, one of the hypothesised primary drivers of disturbance. Comparing structural and non-structural disturbance, our findings conservatively suggest that non-structural disturbance accounts for an area over eighteen times larger than structural disturbance. Our analyses also confirm that accessibility modulates the drivers, spatial distribution and amount of tropical forest disturbance. Rural household density was highest adjacent to rivers whose mouths are close to large urban centres in their most accessible portions. Roadless rivers succumbed to low, unipolar disturbance, whilst road-intersected rivers exhibited higher disturbance footprints at multiple loci. These results suggest that the development trajectory chosen by lowland tropical forest countries can have far-reaching implications for biodiversity.

2.1 Introduction

Despite the fact that tropical forests simultaneously harbour the majority of global terrestrial biodiversity and provide ecosystem services crucial to humanity (Naidoo *et al*., 2008), they continue to be converted or degraded by multiple anthropogenic threats (Wright, 2010). Land-use change is arguably the most significant global scale driver of terrestrial biodiversity loss (Sala, *et al*., 2000). Habitat conversion due to agricultural expansion is identified as the principal mechanism (Tilman *et al*., 2001) and tropical forests bear the brunt of the damage (Gibbs, *et al*., 2010). The degradation and conversion of tropical forests entails a staggering biotic simplification across multiple taxa (Barlow *et al*., 2007; Gibson, *et al*., 2011). On the other hand, merely preventing habitat conversion is insufficient to safeguard tropical biodiversity. Although superficially intact tropical forests may appear to be an unbroken impenetrable mat stretching in all directions, this seductive picture may mask an eerily silent "empty forest" (Redford, 1992) in which species larger than 2kg may be virtually absent due to overhunting (Harrison, 2011). Retaining merely structurally intact forests may thus be a Pyrrhic victory, especially if the loss of functionally crucial taxa results in continued long-term tropical forest degradation (Peres *et al*., 2016).

The Amazon rainforest, 62% of which falls within Brazil, harbours roughly a quarter of global terrestrial biodiversity (Malhi *et al*., 2009) and is the largest contiguous tropical forest on Earth. The Brazilian Amazon experiences the globally highest levels of absolute deforestation (≈2 Mha yr^{-1}, Laurance *et al*., 1998). The "Amazonia Legal" region within Brazil covers an area of ≈ 508,788,238 ha, over 25% of which is protected by legally inhabited reserves including indigenous, sustainable use and extractive reserves (de Marques, *et al*., 2016; IUCN and UNEP-WCMC (2015)) and an additional 21% are protected by indigenous territories.

Cul-de-sac wilderness rivers are pivotal in strategies to protect tropical biodiversity, and can be defined as rivers which do not act as thoroughfares between urban centers (Appendix A). In Amazonia, they are typically first- and second-order tributaries that link major fluvial highways including the Amazonas/Solimões, Negro and Madeira Rivers, with remote and largely uninhabited headwater regions, which retain some of the last remaining tracts of inaccessible tropical forest wildlands on Earth (Peres and Lake, 2003). The unidirectional accessibility of cul-de-sac rivers imposes livelihood constraints on their inhabitants, limiting the spread of anthropogenic disturbance to the lower portions of river basins. The influence of urban centres and the expansion of road networks, however, is beginning to erode their isolation. In particular, the advance of deforestation frontiers along the "arc of deforestation" has culminated in a highly modified forest mosaic in eastern and southern Amazonia. The development of the Trans-Amazon Highway in the 1970s, enabled colonists to bypass fluvial navigational constraints and access hitherto inaccessible forest areas. Brazilian development policy and especially the perverse subsidies and encouragement (by the Instituto Nacional de Colonização e Reforma Agrária (INCRA)) of Amazonian colonisation, have actively fuelled this movement (Binswanger, 1991). Brazilian government commitments to develop hinterland infrastructure colluded with foreign interests is paving the way for extractive industries based of mineral resources (Reid and De Sousa, 2005; Ferreira *et al*. 2015), and make it likely that even currently remote areas will be affected.

Rural extractive communities and isolated households are the only inhabitants of long stretches of cul-de-sac Amazonian rivers. Rural Amazonians are not homogenous, but fall on a socio-ethnic spectrum (Chibnik, 1991) between; (1) Indigenous Amerindian peoples, who have occupied Amazonia for some 10,000 years (Miller, and Nair, 2006). Numbering over 300,000 people, they belonging to around 160 diverse linguistic and cultural groups, ~50 of which are amongst the last remaining uncontacted tribal groups on Earth (Cunha and De Almeida, 2000), but are collectively referred to as indians (*índios*); (2) Neo-colonist groups of mixed European and African descent who migrated into the Amazon within the last three generations, often collectively referred to as *colonos*; and (3) Groups of mixed Amerindian and non-Amerindian descent whose ethnicity, identity, culture and livelihood practices are an intermediate mixture between the aforementioned groups, who are often referred to as river dwelling *caboclos* or *ribeirinhos.*

Rural Amazonian livelihood strategies likewise fall on a spectrum between self-sufficient subsistence extractivism and market-integrated agricultural production. Whilst most households engage in both to varying degrees (Newton *et al*., 2012), high degrees of market integration are often associated with more recent colonists (Stocks *et al*., 2007; Lu *et al*., 2010). Horticultural practices and small-livestock husbandry are largely restricted to comparatively small, heavily modified areas close to homesteads to maximise production and minimise travel costs. By contrast, extractive livelihood practices for subsistence, including hunting and harvesting of other nontimber forest products, require extensive catchment areas. Hunters range over large areas and capture widely distributed and highly mobile prey, without directly modifying forest structure in the short term (but see Peres *et al*., 2016). As predicted by bid-rent theory (Von Thünen, 1966), households engaging primarily in agricultural production, prioritise proximity to urban centers to minimise transport and exchange costs, whereas those engaging primarily in subsistence extractivism, who occupy what Von Thünen termed the “wilderness”, prioritise access to natural resources under lower competitive arenas.

Over 97% of Brazilian Amazonians are non-tribal, and typically of non-indigenous descent (IBGE, 2008). Though often occupying remote areas and adopting elements of indigenous livelihood practices, most *ribeirinhos* are integrated to varying degrees into the Brazilian economy and society and depend on state infrastructure and market goods and services. They are therefore influenced by large-scale sociopolitical and economic processes such as the waxing and waning of the rubber industry, which impelled them to settle remote headwaters with its rise and drew them back into urban areas with its collapse (Hecht and Cockburn, 2010, Parry *et al*., 2010a). Recent government welfare programs and subsidies, such as “Bolsa Familia”, “Luz Para Todos” and “Minha Casa Minha Vida”, have somewhat mitigated the rural exodus.

Different forms of human-induced disturbance in tropical forest regions are almost always considered separately in the conservation science literature (Laurence and Peres, 2006). To our knowledge no study has analysed the threats of both hunting and deforestation in the context of cul-de-sac tropical forest rivers (but see Parry *et al* 2010b for an analysis of extractive activities along eight roadless cul-de-sac rivers). This study uses an array of spatially explicit human population and environmental datasets, including the locations of 633,721 rural Amazonian households, to, firstly, quantify two widespread forms of human structural and non-structural disturbance in tropical forest regions, deforestation and hunting, associated with 45 cul-de-sac rivers. These rivers represent ~ 23,000 km of fluvial distance associated with an area of over 301,000 km^2. Secondly, we examine the relative importance of local and external anthropogenic and environmental factors in explaining the extent of deforestation and hunting. Finally, we discuss the conservation implications of large-scale infrastructure development and socio-demographic changes in Amazonia. By examining truly unipolar rivers alongside those with a degree of road connectivity, we hope to provide insights into the future of an increasingly accessible Amazon.

Due to differences in the aforementioned livelihood practices, we hypothesise that structural disturbance will encompass a small subset of the area affected by non-structural disturbance. We anticipate that highly detectable forest disturbance, will be concentrated near loci of access to external centers of services and trade. Along roadless rivers these loci will be located at river mouths accessible to market towns. By contrast, rivers bisected by roads in their upper sections, along which agricultural settlements have developed in the last three decades, will exhibit a more bimodal pattern of disturbance.

Due to the inaccessibility of our study river-basins, we hypothesise that rural households are the main agents of disturbance along these rivers and that rural population density is the main predictor of disturbance. In addition to population density, the spatial configuration of rural settlements, should also affect patterns of disturbance. Small and large-scale household clustering increases pseudo-interference and exploitative competition (McGinley, 2008, Levi *et al*., 2009), causing hunting catchments to coalesce and therefore reducing the overall hunting footprint and lowering rates of disturbance per household.

As rural households can rely on both extractivism and agriculture, and assuming that rural settlements approximate an ideal-free distribution (as in rural communities elsewhere: Moritz *et al*., 2014), we hypothesize that both environmental and anthropogenic factors drive rural population density, with a higher household density along rivers with more abundant natural resources and easier access to markets. Anthropogenic factors such as roads, increase disturbance both directly and indirectly by increasing rural population density, whereas environmental factors indirectly affect disturbance by either enabling or hindering both rural populations and external actors. For further discussion of the individual hypothesised drivers of disturbance in our study area, see Appendix K.

2.2 Methods

2.2.1 Study area

Our analysis focuses on 45 navigable cul-de-sac rivers distributed across the two largest states in Brazil, representing the largest tropical forest sub-national divisions on Earth, Amazonas and Pará (Fig. 2.1). The former has a total population of 3,938,336, encompasses 157,128,871 ha, has experienced only ~2% deforestation (PRODES, 2009), and has an overall mean rural human population density of ~0.4 inhabitants per km² (IBGE, 2008). The state of Pará has a total population of 7,792,561, covers 124,836,546 ha, has a mean rural population density of ~1.5 inhabitants per km² (IBGE, 2008) and has experienced a deforestation rate that is roughly ten-fold higher (~20%). Mean road density (km/km², including major unpaved roads) across the states of Amazonas and Pará is approximately 0.00219 and 0.00981, respectively. Given Brazil's economic trajectory in frontier expansion and geopolitical commitments to develop the Amazon using massive tax-payer investments (Laurance *et al.*, 2001; Peres, 2001), conservationists often project the future of Amazonas as analogous to present-day Pará. Insights gained from the latter can therefore inform future conservation and development policies in the former.

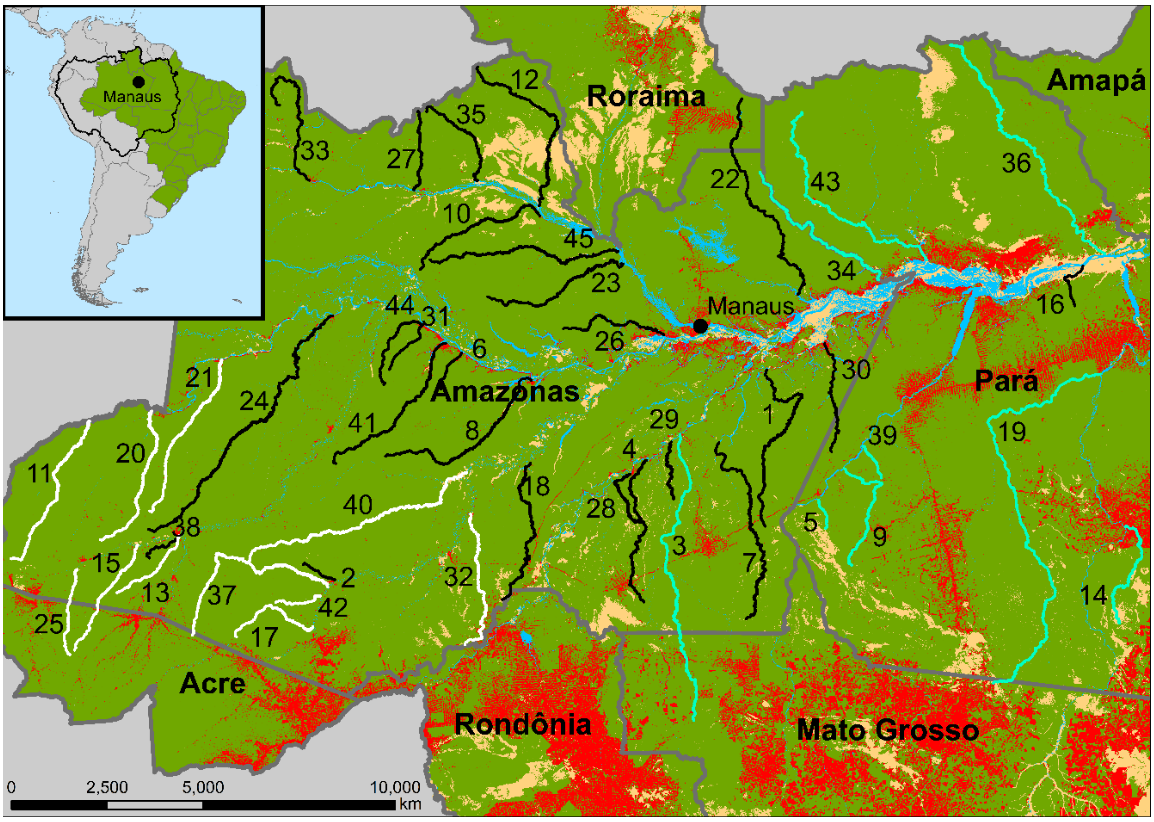

Figure 2.1: *Study area in the Brazilian Amazon, showing the distribution of 45 studied cul-de-sac rivers selected in this study (white, black and blue lines representing white-water, black-water and clear-water rivers, respectively) against a background of land-cover classification in which green indicates forest, red indicates deforestation, peach indicates natural non-forest vegetation, and blue indicates water-bodies (PRODES 2009). Number codes next to rivers correspond to those listed in Table 2.1. Areas outside Brazil are indicated in grey and state boundaries are represented by dark grey lines. Manaus, the capital of the state of Amazonas, is indicated by a black circle. Inset map shows continental scale location of the study area.*

2.2.1 GIS integration and analysis

All GIS data extraction and analysis was undertaken using ArcGIS version 10.3. Shapefiles were projected into the South American Albers Equal Area Conic projection to ensure consistent and accurate area calculations. Statistical Analyses were undertaken using R version 2.1.5. Rivers meeting the following criteria were designated “target rivers” to be used in further analysis: (1) river headwaters are within Brazil; (2) river mouth is within Amazonas or Pará; (3) river is inhabited, with households at least 25 fluvial km upstream from the mouth; (4) river is not a tributary of another target river; (5) river is a cul-de-sac, rather than a fluvial route between towns (a “bead-chain” river), though it may be intersected by one or more roads. Our minimum criterion defining town-hood is 1000 households (see Appendix E).

Three river polyline shapefiles were inspected: (1) the IBGE (2008) "hidro tot linha" shapefile; (2) The Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) Amazon River Basin Land and Stream Drainage Direction Maps (Mayorga *et al*., 2012); and (3) the Hydrosheds hydrographic dataset (Lehner and Grill, 2013a), and later compared to ESRI basemaps. Rivers were digitised from basemaps, because existing shapefiles did not accurately represent the paths and fluvial complexity of small rivers. Where the river course was obstructed by cloud, the ESRI basemap was supplemented with the three aforementioned shapefiles. A total fluvial distance of 22,992 km was digitised. Despite its relative simplicity, the "hidro tot linha" shapefile, which was the most accurate of the available existing river shapefiles, was comparable in terms of associated area, rural households and deforested area, to the digitised rivers. See Appendix B for river digitisation methodology and a detailed comparison between the digitised rivers and existing shapefiles.

Areas of analysis within which we extracted all other variables, were designated per target river. Buffers of 10 km around the digitised rivers were clipped where they met a main bead-chain river and the boundary of the PRODES 2009 deforestation data. To avoid double-counting, buffers were partitioned as follows. Rivers were converted to points at every 1 km of fluvial distance and thiessen polygons were constructed to determine the midpoint between rivers. These polygons were clipped by the extent of the aforementioned buffers (see Appendix C). Using the aforementioned thiessen polygons, river buffers were then divided longitudinally into 25-km segments of fluvial distance, and anthropogenic and environmental variables were extracted both at the segment and whole-river scale.

Two measures of associated area per target river were calculated. The area within river buffers that was not classified in PRODES 2009 as either water, no data, or natural non-forest vegetation was designated "deforestable". The area within river buffers that was not classified in PRODES 2009 as either water or no data was designated "huntable" and/or "inhabitable". As part of the PRODES methodology, pixels obscured by cloud in any given year are classified as water, deforested or non-forest vegetation if this was known from previous years. Residual cloud pixels thus disproportionately represent forest and for the purposes of this analysis, they were treated as such.

The length of polylines representing target rivers was calculated in ArcGIS. Along each target river, ten equally spaced points were created. At each point, the width of the river perpendicular to the direction of flow was measured on the ESRI basemap. An average value per river was taken from these measurements. To obtain an average flow accumulation value per river the ORNL DAAC flow accumulation database, with a cell size of 500 m, was used. Sample points were created in the midpoint of every 25-km fluvial segment. The highest flow accumulation value within a 1-km buffer of the sample point was taken. This was necessary to capture the flow accumulation value for the target river itself, because the flow accumulation dataset did not perfectly match the digitised river. A mean of the sample values was taken for each river. To calculate river gradient, Shuttle Radar Topography Mission (SRTM) 90-m resolution elevation data (Jarvis *et al.*, 2008) was used. The minimum elevation value within a 200-m buffer of the start and endpoint of each river segment was taken. A smaller buffer was used for elevation than for flow accumulation because the SRTM data is finer scale. Mean slope was then calculated by dividing the elevational difference between the start and end of rivers, by the total nonlinear fluvial length. A slope value per segment was calculated as the cumulative elevational change between the segment and the river mouth, divided by the fluvial distance to the river mouth.

Three data sources were used to locate waterfalls: (1) the Hydrofalls Global Waterfalls database (Lehner and Grill, 2013b); (2) the Woods Hole datasets for Amazonia (http://www.whrc.org/mapping/lba_datasets/lba.html, accessed 01/10/2015); and (3) the Geonames geographical database (http://www.geonames.org/, accessed 01/10/2015). Due to the remoteness of the target rivers, the aforementioned datasets were incomplete. Rivers were inspected by eye using ESRI basemaps. Where a waterfall was visually apparent, it was digitised regardless of whether it appeared in the above datasets (see Appendix L). Where more than one dataset agreed on the location of a waterfall, it was digitised even if it was not apparent from basemaps. The number of waterfalls and large rapids were summed both for each river and each river segment, by adding all waterfalls/rapids between each segment and the river mouth.

Deforestation was assessed using the PRODES 2009 raster dataset. To calculate deforested area, all cells other than deforested were converted to a polygon and erased from the river buffers. PRODES 2009 deforestation data was compared with other years and validated against the Global Forest Change dataset (Hansen *et al.,* 2013*)* (see Appendix D).

Rural households were extracted from a spatially explicit dataset from the 2007-2009 IBGE population census of rural households in the states of Amazonas, Pará, Acre, Mato Grosso, Rondônia and Roraima. Each point represents one permanent private rural household. This dataset was validated against publicly available IBGE 2007 census data (see Appendix D). In addition to summing all households per river and segment, the observed average nearest neighbour distance, which measures the degree of small scale clustering, was calculated. The Nearest Neighbour Index was not chosen because the extremely heterogeneous river shapes and sizes makes inter-comparison problematic (ESRI documentation for the Average Nearest Neighbour Tool, http://resources.arcgis.com/en/help/main/10.1/index.html#//005p00000008000000). A measure of the extent of occupancy or large scale spread was calculated by summing for each river the area of the thiessen polygons containing at least one household.

Tropical game hunters are typically central place foragers, whereby hunting effort declines exponentially with distance from the household, with almost no hunts beyond 10km (Alvard *et al.,* 1997; Siren *et al.,* 2004; Peres and Nascimento, 2006; Ohl-Schacherer *et al.,* 2007; Smith, 2008). We therefore defined all forest, deforested and natural non-forest vegetation pixels within a 10-km buffer of any rural household as the hunting catchment. Deforested and non-forest areas were included because many hunts occur opportunistically in and around agricultural areas (Parry *et al.*, 2009; Chapter 3).

Target rivers relate to market towns of varying sizes at varying distances from their mouths. We therefore sought a variable that captures, in a way relevant to the forces acting on rural Amazonians, the degree to which river dwellers maintain access to urban centres by creating an urban proximity index (UP), applied to an entire river rather than each fluvial segment. For a given town and river, this index is expressed as the size of the town (number of households, U_{size}) divided by the number of days travel to the river mouth, $D_{fluvial}$ ($UP = U_{size}/D_{fluvial} + 1$). The UP indices of the two towns closest to the river mouth, were then summed per target river. A day's travel was taken to be 50 km of fluvial distance for a rural Amazonian using a canoe with a small outboard motor (locally, *rabeta*), as validated by our own field experience. For more methodological details, see Appendix E.

IBGE data on paved and unpaved roads was used to create two alternative road variables; road length and road intersections. Roads designated as "planned" were excluded by default, but inspected using basemaps. Where unmapped roads (paved or otherwise) were clearly apparent in the vicinity of target rivers, they were digitised. The length of roads within segmented river buffers was calculated, and a road intersection point was digitised wherever a road crossed a target river.

Polygons representing all areas of commercial and artisanal mining claims were created using data from SIGMINE (2015). Despite a mismatch between polygons representing registered mines, and visually obvious mining disturbance, the available polygons were preferred to digitisation of mining sites, in order to avoid analytic circularity (see Appendix F)

Registered airports and airstrips from the Woods Hole datasets for Amazonia were supplemented with unregistered airstrips identified from ESRI basemaps. We do not consider this to be circular as the area of deforestation represented by a rural airstrip is small, but easily identified (see appendix G). Urban airports were excluded from analysis as they are a reflection of town size, which is better captured by the urban proximity index described above.

Protected area polygons were downloaded from the World Database on Protected Areas (WDPA 2015) and then merged and dissolved. Protected areas of different types may overlap to a minor extent, but were not differentiated. For example, over 2.6% of all forest reserves in Brazilian Amazonia fall under both inhabited and uninhabited PA categories.

A nine level ordinal classification of soil fertility for the Brazilian Amazon (Laurance *et al.*, 2002) was used to calculate an area-weighted mean soil fertility per river buffer segment. This was preferred to an assessment of river geochemistry/colour (see Appendix H). Upon inspection of the distribution of soil fertility within our study area, the lowest class, despite being termed soils "with no potential for agriculture", often overlapped water bodies. Thus two alternative area-weighted soil fertility variables were created, including or excluding the lowest class. Data from the Tropical Rainfall Measuring Mission (Simpson *et al*., 1996) was used to calculate the mean annual precipitation per segmented river buffer.

2.2.2 Data analysis

2.2.2.1 Patterns of structural and non-structural disturbance

The area associated with each river and river segment was separated into disturbance categories as (1) both deforested and hunted; (2) only hunted; (3) only deforested; and (4) neither deforested nor hunted, and converted to a percentage of total area. All natural non-forest vegetation was considered as potentially subjected to hunting, but not deforestation. Deforestable area per river was thus on average 3.0 ± 1.2% smaller than huntable areas, and these were averaged to calculate the percentage of both hunted and deforested areas. A Kruskal-Wallis test was then performed to determine if the area of different disturbance categories were significantly different per river. Rivers were grouped by anthropogenic categories reflecting whether their area of analysis included (1) both towns and roads; (2) only roads; (3) only towns; and (4) neither. A Kruskal-Wallis test was performed to determine if the area of deforestation per river differed significantly between anthropogenic categories.

Roads often emanate from towns near river mouths, making it difficult to disentangle the effect of roads from that of urban infrastructure. Rivers were therefore separated into those with and without significant road intersections upstream from the river mouth (hereafter, road-intersected and roadless rivers, respectively). The proportion of deforestation and road density within each 25-km fluvial segment was calculated.

Mann–Whitney–Wilcoxon tests were used to compare levels of absolute and proportional deforestation between rivers whose mouths were located in either Amazonas or Pará. As our sample size was uneven between states, which covaried with a number of our other explanatory variables, we did not include "state" as a predictor in models.

2.2.2.2 Models of rural household density and deforestation

Generalised Linear Models (GLMs) and Generalised Linear Mixed Effects Models (GLMMs) were created to separately determine the drivers of rural population density and deforestation at the scale of whole rivers and fluvial segments, respectively. A Spearman correlation matrix was created to check for collinearity between continuous variables. Where explanatory variables were highly correlated (Spearman's Rho > 0.7), either the most theoretically appropriate variable was included in models or, if variables were equally appropriate, both variables were modelled separately and the model with the lower AIC was retained. Neither soil fertility scores were retained in any model. Road length resulted in a lower AIC than road intercepts.

Histograms were plotted to check variable distributions, which in most cases were right-skewed. A two-way boxcox test (Box and Cox, 1964) was used to guide the appropriate transformation of the dependent variables relative to the independent variables where lambda values close to zero indicate that a log transformation is appropriate. Explanatory variables were converted into landscape-scale densities, rates or proportions wherever appropriate. All continuous variables were scaled and centred to aid model convergence and comparisons of effect sizes.

GLMs and GLMMs separately treated area of deforestation and the number of rural households as count responses with an associated log-transformed exposure variable (deforestable or inhabitable area). To account for the nested structure of segmented river data, GLMMs included the river ID as a random effect. Negative Binomial models were chosen because Poisson models with a log link revealed overdispersion. They also have an advantage over Quasipoisson models that AIC values, rather than QuasiAIC values, can be used to evaluate models. The hunted area was derived directly from household locations. It would therefore be circular to model it as a response variable using households as an explanatory variable, so hunted area was not modelled.

The initial whole-river global models of deforestation included as explanatory variables river width, soil fertility (including and excluding the lowest class, tested separately), rainfall, slope, density of waterfalls and large rapids, density of rural households, nearest neighbour distance between households, UP index, proportion of legally protected area, density of airports and airstrips (combined), density of roads and road intersections (examined separately), density of commercial and artisanal mines (separate variables included simultaneously). Initial whole-river global household models included as explanatory variables all of the above, except for rural household density and nearest neighbour distance between households. In GLMMs, the distance between each segment and the river mouth was also included as an explanatory variable. The nearest neighbour distance between rural households was excluded from segment models because 51% of river segments were uninhabited.

Models were selected using supervised backwards stepwise deletion. Explanatory variables with the highest p-value was sequentially removed, unless this resulted in an increase in ΔAIC > 2, until a minimum adequate model was reached. Variables were then sequentially deleted and ΔAIC was used to determine if additional deletions were warranted.

2.3 Results

Our 45 target rivers (Table 2.1) represent a combined fluvial distance of 22,992 km (mean = 511.0 ± 12.3 km), with an associated area of 301,641 km² (mean = 6,703.1 ± 578.0 km²) inhabited by a total of 21,758 rural households (mean = 484.0 ± 65.2). Land-cover adjacent to these rivers was distributed significantly unevenly between the four disturbance categories (Kruskal-Wallis test, $p < 0.001$, Figs. 2.2, 2.3 and 2.5). The combined hunted area associated with all rivers was 142,280 km² (mean per river = 3,162 ± 299 km²), over 18 times larger than the combined deforested area of 7,817 km² (mean = 174 ± 31 km²).

On average, nearly half of the area associated with these rivers is neither deforested nor hunted (mean = 48.7 ± 3.0%), with nearly half of the area only hunted (mean = 48.4 ± 3.0%) and a small proportion both hunted and deforested (mean = 2.7 ± 0.5%). A very small proportion was only deforested (mean = 0.18 ± 0.04%), and a small proportion of the deforested areas did not fall within hunted areas (mean =10.4 ± 1.8%).

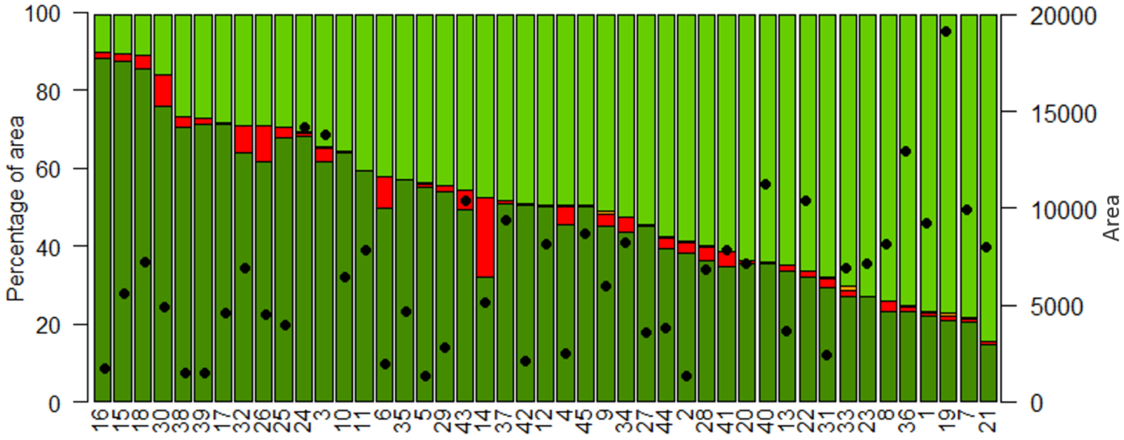

***Figure 2.2**: Proportional areas adjacent to each study river within each human disturbance category. Rivers are ordered by total level of disturbance, from lowest to highest. Stacked bars represent the percentage of area and bar colour indicates disturbance category, where undisturbed, hunted only, deforested only, and both hunted and deforested are dark green, light green, orange and red, respectively. The total adjacent area (km²) per river is indicated by black circles.*

***Table 2.1**: Study rivers and associated traits. River bifurcations are indicated by hyphenated names. State = the state in which the river mouth is located. AM = Amazonas. PA = Para. Length = fluvial length (m). Width = mean width (m). Slope = change in elevation (m) per 100,000 m of fluvial length. Falls = number of waterfalls and large rapids. Fert = mean soil fertility. Chem = river colour classification. Area = inhabitable area (km^2). Defor = deforested area (km^2). Hunt = hunted area (km^2). Protect = protected area (km^2). Hhs = number of rural households. NND = Mean nearest neighbour distance between rural households. Town = name of nearest market town. Urban = the urban proximity score. Air = number of rural airstrips. Road = length of road (m). Mine = area of commercial mines (km^2).*

name	id	state	length	width	slope	falls	fert	chem	area	defor	hunt	protect	hhs	NND	town	urban	air	road	mine
Abacaxis	1	AM	706166	351	29	0	3.48	black	9359	103	2158	2256	293	151	Nova Olinda Do Norte	1744	0	21085	0
Agua Preta	2	AM	116142	25	66	0	1.81	black	1556	44	642	975	121	136	Pauini	2103	1	7364	0
Aripuanã	3	AM	898556	218	21	0	3.35	clear	13840	520	9064	4871	684	432	Novo Aripuanã	3357	2	329651	0
Atininga	4	AM	301603	55	15	0	3.39	black	2731	136	1348	0	185	204	Manicoré	3102	1	34590	0
Cabitutu	5	PA	96112	26	67	0	3.03	clear	1540	16	848	1550	173	71	Jacareacanga	2932	1	0	0
Caiambe	6	AM	142325	256	40	0	2.55	black	2119	171	1227	0	506	60	Tefé	6079	0	0	0
Canuma_ Sucunduri	7	AM	692045	125	25	2	3.33	black	10124	103	2166	4642	188	369	Novo Aripuanã	1140	1	46460	0
Coarí	8	AM	707064	774	11	0	2.58	black	8360	234	2154	63	399	183	Coari	11148	1	44537	0
Crepori_ Marupa	9	PA	377913	94	43	0	3.54	clear	6136	253	2963	5785	496	54	Jacareacanga	3183	11	28257	31
Cuiuní	10	AM	537734	100	9	0	2.73	black	6592	36	4240	313	505	255	Barcelos	2462	1	17105	0
Curuça	11	AM	756048	105	20	1	3.16	white	7983	15	4766	6549	250	449	Atalaia Do Norte	625	0	0	0
Demini	12	AM	641567	167	79	10	3.03	black	8841	17	4207	4977	522	203	Barcelos	1532	1	31122	0
Eiru	13	AM	321653	43	29	0	2.93	white	3845	61	1356	2781	231	196	Eirunepé	4637	0	0	0
Fresco_ Riozinho	14	PA	395109	92	71	9	3.22	clear	5733	1090	2795	4362	1007	271	São Félix Do Xingu	8738	7	348303	0
Gregório_ Salvador	15	AM	465520	50	44	0	4.49	white	5745	115	5134	4197	509	232	Eirunepé	1009	1	21632	0
Guajará	16	PA	141355	59	49	0	3.01	black	2405	28	1721	1932	250	180	Prainha	2284	0	0	0
Inauini	17	AM	371095	48	36	0	3.52	white	4727	22	3402	3103	412	236	Boca Do Acre	2478	0	0	0
Ipixuna	18	AM	626979	122	8	0	1.98	black	7522	260	6570	3141	542	338	Tapauá	2410	1	191753	0
Iriri	19	PA	1132169	411	17	18	2.97	clear	19346	397	4230	19203	90	1864	Altamira	7547	11	167581	0
Itaquai	20	AM	664836	97	19	0	3.16	white	7301	55	2663	6329	359	55	Atalaia Do Norte	3039	0	30477	0
Jandiatuba	21	AM	750974	92	20	0	3.13	white	8087	53	1257	4463	326	74	São Paulo De Olivença	2241	1	11658	0
Jaú	23	AM	597350	86	9	0	2.21	black	7289	23	1977	7375	88	388	Novo Airão	1108	0	0	0
Jutai_ Jutaizinho	24	AM	1229539	181	15	0	2.64	black	14276	122	9916	9984	871	346	Jutaí	2752	0	6231	0
Liberdade	25	AM	330024	39	41	0	4.71	white	4123	106	2914	2348	405	275	Ipixuna	1234	0	22265	0
Manacapuru	26	AM	349749	544	13	0	2.68	black	4689	432	3338	238	1071	141	Manacapuru	12940	0	89262	0
Marauia	27	AM	280704	60	188	4	3.63	black	3725	16	1703	3468	186	63	Sta Isabel Do Rio Negro	1516	0	3602	0
Maricoré	28	AM	594373	97	13	4	3.32	black	7100	277	2776	538	304	139	Manicoré	4387	0	60587	0

name	id	state	length	width	slope	falls	fert	chem	area	defor	hunt	prot	hhs	NND	town	urban	air	road	mine
Maues_ Amanã	30	AM	320717	645	33	1	3.65	black	5023	407	4233	3357	1496	152	Maués	5489	14	22013	25
Miratu	31	AM	176674	36	33	0	2.61	black	2589	66	826	108	93	263	Uarini	1964	0	10826	0
Mucuim	32	AM	559739	65	11	0	1.99	white	7081	495	5016	4724	475	563	Canutama	2289	0	442015	0
Negro_ Xie	33	AM	452316	410	13	7	2.79	black	7055	200	2022	5719	1556	11	São Gabriel Da Cachoeira	4005	1	32913	0
Padauari_ Marari	35	AM	387347	87	73	3	2.71	black	4907	13	2765	1845	168	588	Sta Isabel Do Rio Negro	918	0	0	0
Parú	36	PA	854873	150	43	8	3.64	clear	13310	177	3207	11055	1000	98	Almeirim	3916	3	72833	35
Pauini	37	AM	831273	92	15	0	3.46	white	9472	75	4906	290	279	432	Pauini	1879	0	18407	0
Preto	38	AM	127855	18	81	0	3.45	black	1665	49	1225	860	162	71	Eirunepé	3526	0	0	0
Rato	39	PA	114164	29	95	0	3.94	clear	1706	29	1246	1619	29	903	Jacareacanga	3801	3	0	49
Tapura_ Tapaua	40	AM	969769	152	13	0	2.45	white	11550	42	4064	6588	421	619	Canutama	618	0	0	0
Tefé	41	AM	657522	669	16	0	2.68	black	8025	321	3086	1368	1044	84	Tefé	10724	1	24131	0
Teuini	42	AM	181253	36	50	0	2.90	white	2274	8	1162	1386	76	500	Pauini	1693	0	0	0
Trombetas_ Mapuera_ Tauini	43	PA	630301	368	37	4	3.44	clear	10490	537	5700	9573	2107	154	Oriximiná	11862	4	89202	48
Uarini	44	AM	310949	256	21	0	2.59	black	4020	121	1698	1070	375	82	Uarini	1905	0	5459	0
Unini	45	AM	692669	285	8	0	2.08	black	8922	35	4449	9171	363	220	Novo Airão	1052	0	0	0

2.3.1 Distribution of structural and non-structural disturbance

Hunted areas were widely distributed both longitudinally and laterally along our study rivers (Fig. 2.3). In the case of roadless rivers, areas affected by deforestation were unipolar, concentrated near the river mouths and areas immediately adjacent to the riverbanks, and occupied a small subset of the hunted areas. However, rivers intersected by roads far upstream from their mouths, exhibited a multimodal pattern of deforestation, because road intersections across river headwaters were associated with recent loci of more aggressive deforestation (Fig. 2.4).

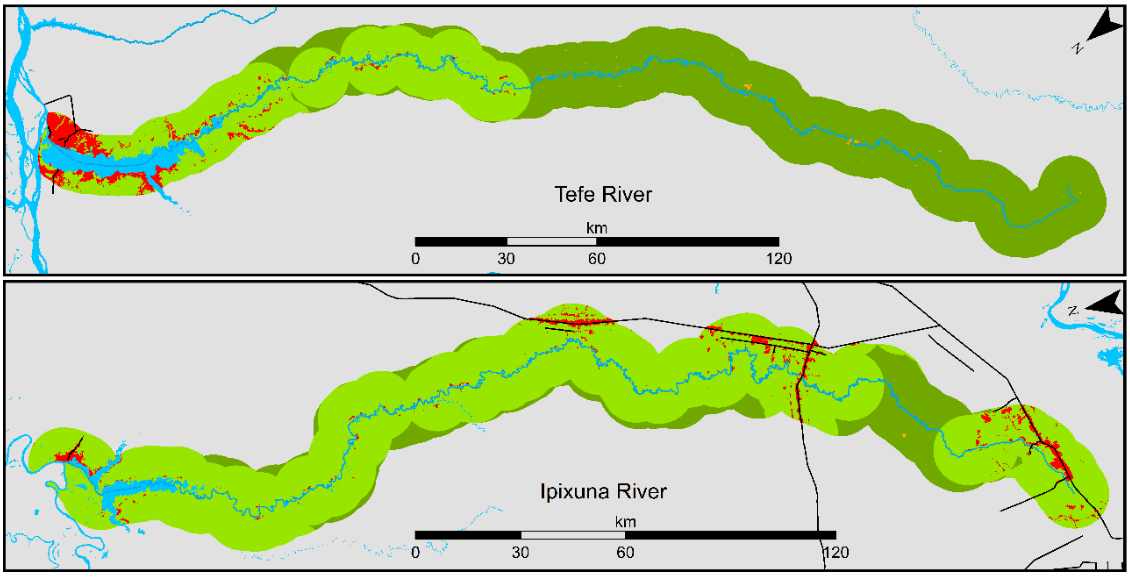

***Figure 2.3**: Pattern of anthropogenic disturbance adjacent to two example roadless (top panel) and road-intersected rivers (bottom panel), representing areas defined by PRODES 2009 as water in blue, areas outside the zone of analysis in grey, areas neither hunted nor deforested in dark green, areas hunted but not deforested in light green, areas deforested but not hunted in orange and areas both deforested and hunted in red. Black and dark blue lines indicate roads and the main course of rivers respectively.*

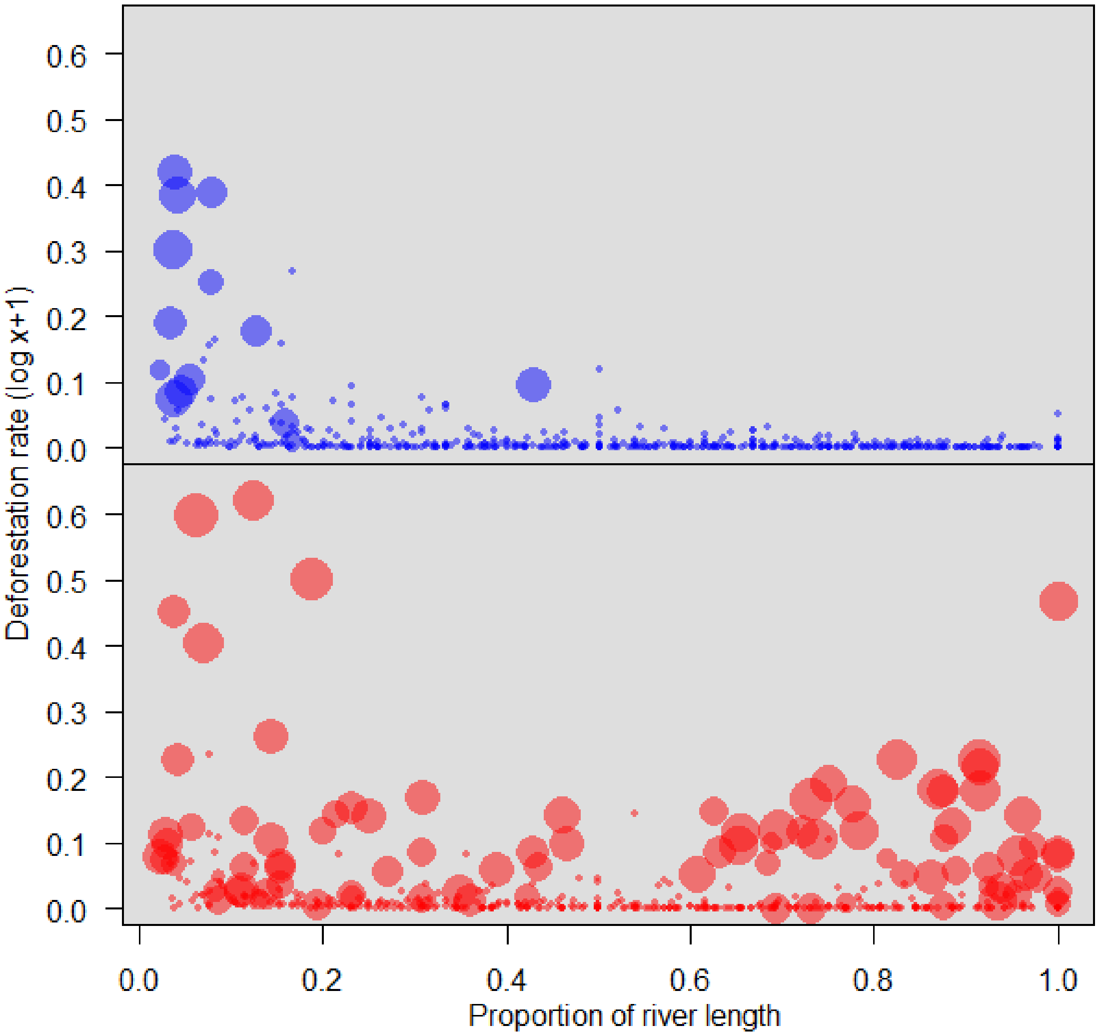

***Figure 2.4**: Longitudinal patterns of deforestation along roadless (top panel) and road-intersected (bottom panel) study rivers upstream from the river mouth. The deforestation rate (log x+1) within every 25-km fluvial segment is plotted against the relative distance from the river mouth, ordered from nearest to farthest. Circle size indicates the road density (log x+1), with larger circles indicating higher density.*

2.3.2 The effects of disturbance category and state

Comparing rivers grouped by anthropogenic disturbance category (Fig. 2.5, Panel A), rivers that included roads and towns within their areas of analysis had significantly larger absolute ($p < 0.001$) and proportional areas ($p < 0.05$) of deforestation than those that included only one or none of these. Rivers with neither roads nor towns within their area of analysis on average had experienced only 1.5 ± 0.6% of deforestation. A single river with a town but no roads experienced 1.6% of deforestation. Rivers with roads but no towns experienced 2.1 ± 0.6% of deforestation, and those with roads and towns experienced 2.8 ± 1.1% of deforestation.

Neither absolute nor proportional deforestation were significantly different between rivers whose mouths are located in either the state of Amazonas or Pará (Fig. 2.5. Panel B. Wilcoxon tests, $p > 0.05$ in both cases).

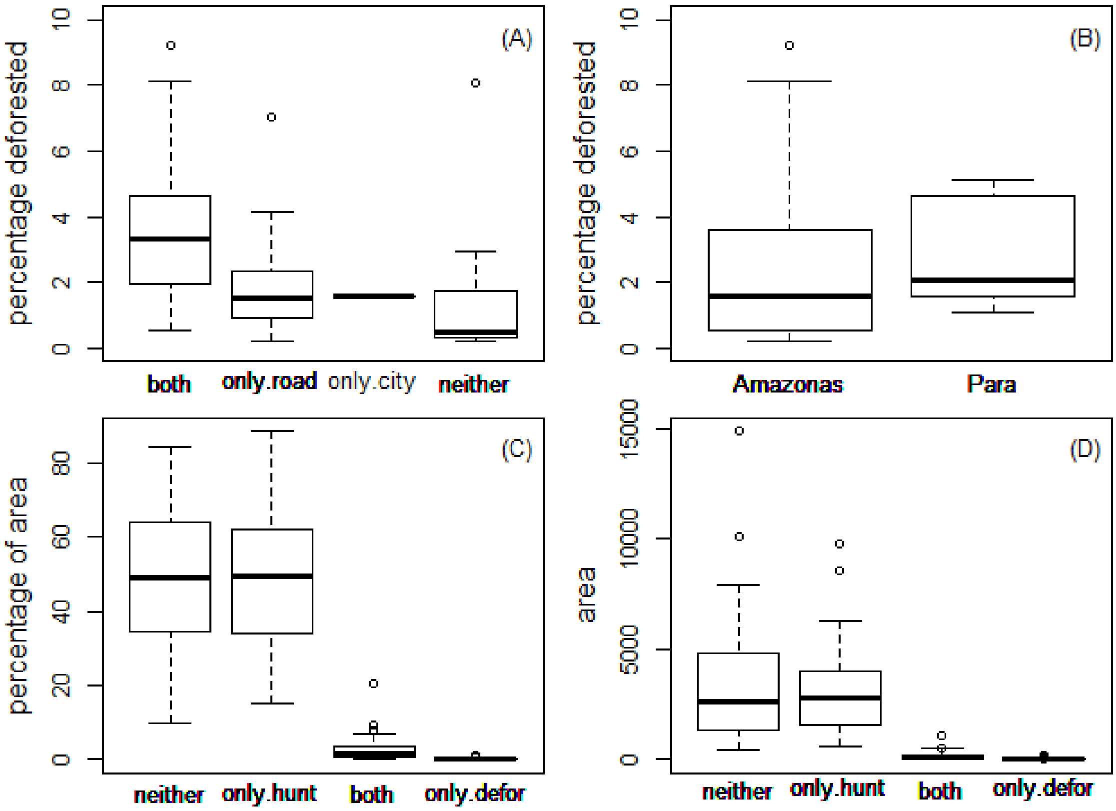

***Figure 2.5**: Comparison of (A) percentage deforestation for rivers grouped by anthropogenic category; (B) percentage deforestation for rivers grouped by state; (C) percentage of the associated area of all rivers split by disturbance category; and (D) the associated area (km^2) of all rivers split by disturbance category.*

2.3.3 Drivers of rural population density and deforestation

At the scale of both whole river basins and of fluvial segments, environmental variables including river width, navigability (as indicated by both river slope and the presence of waterfalls and large rapids), and soil fertility and were all discarded from both deforestation and household models. High mean annual precipitation did, however, reduce deforestation rates at the scale of whole rivers (Fig. 2.6. $p < 0.05$). By contrast, anthropogenic variables including both road and rural household density were strong positive predictors of deforestation rate at the scale of whole rivers ($p < 0.001$ in both cases) and fluvial segments ($p < 0.001$ and $p < 0.05$, respectively), whilst fluvial distance from the river mouth had strong negative effects on both household density and deforestation rate at the scale of fluvial segments ($p < 0.001$ in both cases).

Rural household density at the scale of whole rivers was highest in rivers close to urban centres ($p < 0.001$), with a lower density of commercial mines ($p < 0.01$), but with a higher density of airstrips ($p < 0.05$). At the scale of fluvial segments, however, road density replaced urban proximity as the primary driver ($p < 0.001$) and the density or commercial mining site was discarded. Legally protected areas had no effect on household density, but negatively influenced deforestation rates at the level of whole rivers (< 0.001). Rural airstrips increased the density of both rural households and deforestation at the scale of both whole rivers ($p < 0.05$ in both cases) and fluvial segments ($p < 0.01$ and $p = 0.05$, respectively).

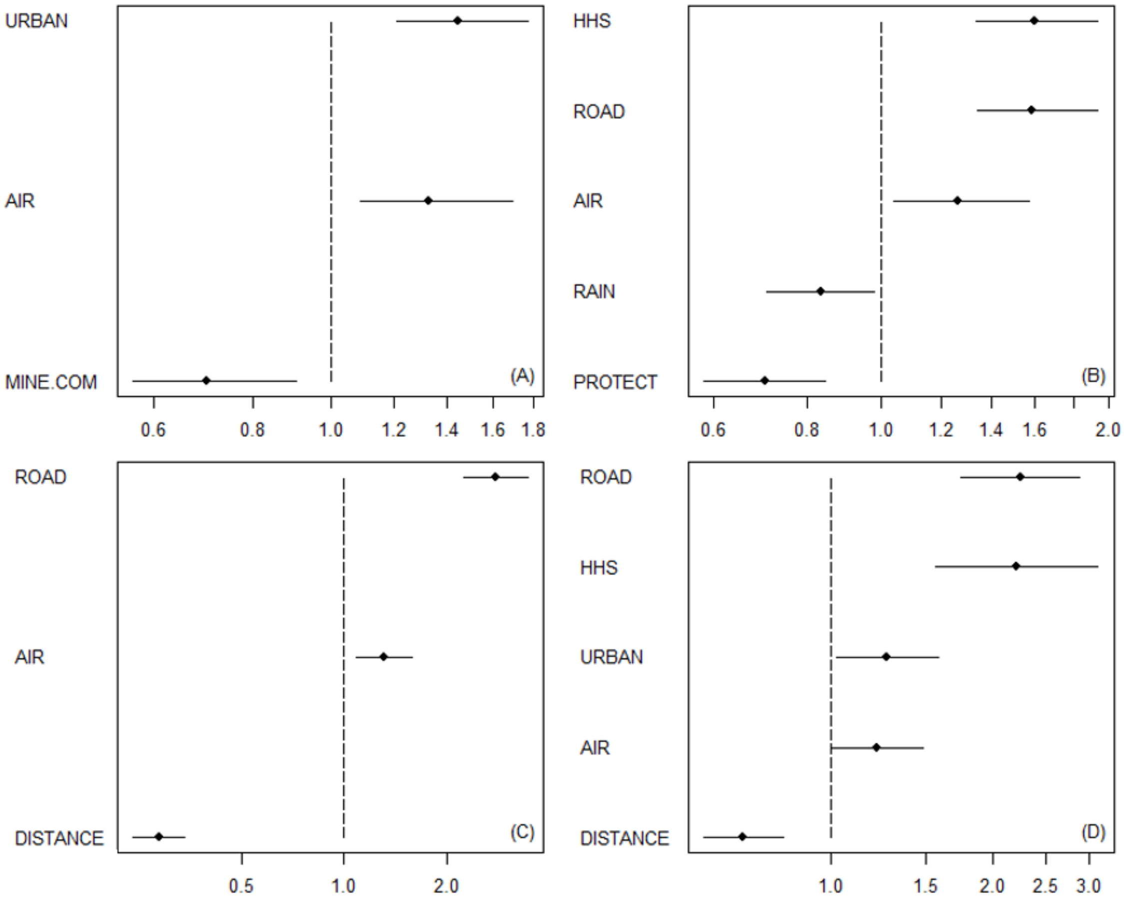

Figure 2.6: *Odds ratios and 95% confidence intervals for the explanatory variables retained in the best performing GLMs of (A) rural household at the scale of whole rivers; (B) deforestation rate at the scale of whole rivers; (C) rural households at the scale of fluvial segments; and (D) deforestation rate at the scale of fluvial segments. URBAN = the urban proximity score, AIR = rural airstrips, MINE.COM = commercial mines, ROAD = road density, DISTANCE = fluvial distance from the river mouth, HHS = rural household density, RAIN = mean annual rainfall, PROTECT = proportion of legally protected areas.*

2.4 Discussion

2.4.1 Hinterland accessibility

Physical accessibility is one of the most important overarching moderators of anthropogenic disturbance in all remaining lowland tropical forest wilderness regions. Roadless rivers, even if they are highly navigable, are inherently protected by the passive defence costs and difficulty of long-distance fluvial travel, which largely constrains anthropogenic disturbance, especially deforestation, to lower reaches of river basins and the vicinity of the river banks. Roadless cul-de-sac rivers in our study not only suffered lower levels of disturbance, but tended to show a clear unipolar pattern of human disturbance. Likewise, GLMMs showed that deforestation was strongly negatively influenced by distance to the river mouth, and strongly positively influenced by both paved or unpaved roads and airstrips. This suggests that once external actors introduce alternative means of efficient access via airstrips or roads, fluvial navigation barriers can be sidestepped and otherwise remote headwaters can be rapidly colonised. The size and prosperity of urban centres, which were an important driver of rural population density, are themselves governed both by the environmental characteristics of their location, such as the fertility of the soil, but more importantly by their strategic position within the fluvial Amazonian transport network. It is no accident that Manaus, the state capital of Amazonas, is located at the confluence between the Amazon/Solimoes and the Negro Rivers, which are the largest rivers in the Amazon.

2.4.2 Drivers of deforestation

Several studies have emphasised the importance of roads (Kirby *et al*., 2006; Adeney *et al*., 2009), population growth, shifting cultivation, agricultural expansion (Allen and Barnes, 1985; Brady, 1996), and dry season severity (Laurance *et al*., 2002) as drivers of tropical deforestation. By contrast, rural airstrips are rarely considered in analyses of anthropogenic disturbance (but see Dávalos *et al*., 2011). We found that the drivers and enablers of deforestation were heterogeneous, including baseline environmental variables, local and external anthropogenic variables, as well as the absence of legal protection.

Environmental variables were, however, overall weak predictors of deforestation, with mean annual precipitation being the only environmental variable retained in our deforestation models. This weakness may reflect the fact that these variables act indirectly, with their explanatory power captured by the anthropogenic variables they influence. For example, high rainfall areas are less vulnerable to deforestation, in part because they pose prohibitive logistical challenges to road-builders and year-round road access. Furthermore, though we attempted to include the most relevant environmental variables, it is possible that others such as rainfall seasonality or primary productivity, are more important determinants of human population density and deforestation

(Laurance *et al.,* 2002). Despite their wide geographic distribution, the least deforested target rivers are clustered in the most aseasonal and least accessible western portions of Brazilian Amazonia. This may reflect an uncaptured environmental variable, or the position of the rivers within the wider transport network.

There is some debate over the relative importance of different agents of deforestation, including smallholders vs. largeholders and long-term residents vs recent colonists. There is evidence that the drivers of tropical forest disturbance are increasingly decoupled from small-scale traditional agriculturalists and connected to urban expansion and wealthier actors supplying external markets (Rudel *et al*., 2009; DeFries *et al*., 2010). On the other hand, resettled smallholders account for much of Amazonian forest conversion and fires in the past few decades and the share of Brazilian Amazonian deforestation attributable to smallholders, has increased over the past decade (Godar *et al*., 2014; Schneider and Peres, 2015).

We found that both rural population density and other anthropogenic variables linked to external actors, such as roads and airstrips, drive deforestation, whereas urban areas were relatively weak direct drivers. There were only 484 rural households per target river on average, whereas a modestly sized Amazonian town such as Tefé contains nearly 10,000 households. The effect of this population disparity is moderated by the sparse and well dispersed rural population vs a dense urban population, but magnified by differential access to capital. Per capita GDP of urban Amazonians in 1995 was over twice that of rural Amazonians (Margulis, 2004). Densely clustered urban Amazonians are typically in the wage labour sector and can afford machinery such as chainsaws required to clear large agricultural areas for commercial agriculture. Urbanites, Amazonian or otherwise, are similarly responsible for infrastructure such as roads and airstrips, which extend urban influence but are beyond the means of rural families. Baseline deforestation rates in the absence of urban clusters and other external forces is likely so low (Fig. 2.5), that its signal would be lost amidst the background noise of non-resident anthropogenic impacts.

These apparently contradictory findings are in fact reconcilable. Firstly, small-scale farmers (identified by the aforementioned studies) own properties of up to 100ha and include primarily recent immigrants. One may either conceive of them as either relatively poor, local, rural agriculturalists, or as external, market-integrated, commercial producers. Secondly, actors may alter their livelihoods in response to increased market-integration and thus external drivers may transform the activities of local actors (Walker, 2003). Thirdly, we were unable to distinguish the socio-ethnic background of rural households. Had we done so, we may have been able to attribute different disturbance footprints to different agents. Fourthly, our explanatory variables were closely interlinked and we found that urban and other external anthropogenic variables drove rural household density.

2.4.3 Drivers of rural population density

Proximity to urban centres was the key determinant of rural population density at the scale of whole rivers, whilst road density and distance to the river mouth — which is a proxy of access to markets and public services — were the key drivers at the fluvial segment scale. The low explanatory power of environmental variables defied our expectations. We anticipated that along remote rivers, where inhabitants presumably rely heavily on natural resources and fluvial navigation, population density would reflect both anthropogenic and environmental factors. The livelihood impact of environmental variables on rural Amazonians is summarised by the fact that low productivity black-water rivers are dubbed "hunger rivers" by local inhabitants (cf. Janzen, 1974).

The benefits of occupying high fertility watersheds may be mitigated by more prevalent crop diseases, raiders and pests and parasitic human disease vectors (Janzen, 1974; Tadei *et al*., 1998). Equally, we may need to reassess our notions of what motivates rural Amazonians in their settlement choices. Arguably, most modern rural Amazonians are more market than subsistence-oriented. They often value forest resources more for their cash value than for subsistence and make settlement and livelihood decisions accordingly. A major non-indigenous population influx into remote portions of Amazonia during the heyday of natural rubber exploitation was driven by a highly saleable market commodity but this was rapidly reversed with the collapse of its price (Hecht and Cockburn, 2010; Parry *et al*., 2010 a, b). Most of those who did not relocate to urban centres are still highly reliant on them. As such, the most attractive rivers to rural Amazonians are those connected to large town, and not necessarily those containing abundant natural resources.

2.4.4 Patterns of disturbance

The results of our study highlight the fact that hunting represents a far more widespread and diffuse phenomenon than deforestation. The patterns of deforestation and hunting largely met our expectations, with the latter accounting for an area over 18-fold larger than that of clear-cuts. As noted, structural disturbance tends to be clustered near the mouth of Amazonian rivers, except where external anthropogenic factors such as roads create additional satellite nodes of deforestation (Fig. 2.3 and 2.4). By contrast, even apparently pristine and remote areas can be affected by non-structural anthropogenic disturbance that is often difficult to detect.

As a testament to the remoteness of our study rivers, almost half of the area adjacent to them was neither deforested nor hunted. This is a conservative estimate of the hunting footprint along these rivers because we do not account for likely incursions of commercial hunters supplying the urban wildmeat trade, whose clandestine activities are difficult to quantify. Nor do we account for multi-day hunting forays by subsistence hunters. Had we done so, the extent of hunting along our studied rivers would have been far higher (cf. Peres and Lake 2003). Commercial hunters are anticipated to make less frequent, multiple-day hunts, travel much greater distances, kill more animals per trip and live in or near to a town, where they trade their catch. For example, harvesting of aquatic and terrestrial wildlife by non-resident hunters can continue into headwater regions, hundreds of kilometers beyond the last household on any given river (Parry *et al*., 2010). Given our finding that deforestation is strongly associated with urban and external actors, it may be appropriate to both broaden our conception of hunting agents by incorporating urban households and to account for fluvial access.

Hunting and deforestation have markedly different effects on tropical forest biodiversity. Deforested areas are a vastly simplified habitat, host to a tiny proportion of the formerly resident species (Lawton *et al.,* 1998; Fitzherbert *et al.,* 2008; Gardner *et al.,* 2010). By contrast, hunting leaves intact the vast majority of the biotic assemblage, and disproportionately concentrated on vertebrate species >1kg (Peres, 2000). Even moderate hunting pressure can functionally eliminate the largest, least fecund species, with detrimental repercussions for ecosystem functions including seed dispersal (Muller-Landau, 2007).

2.4.5 Conservation implications and future research

The detrimental impact of roads is a recurring theme in this study. Not only were roads strong drivers of deforestation and rural household density along our study rivers, but they were associated with incongruous land-use change far into otherwise inaccessible headwaters. Nevertheless, our results potentially understate the detrimental effects of roads because (1) they are more efficient, flexible and cost-effective means of access than rivers (Knowles, 2006) and therefore facilitate cryptic disturbance by non-resident loggers and hunters (Peres et al., 2006), which was not accounted for here; (2) roads influence not only human population density, but also regional demographic make-up. They attract settlements comprised primarily of agriculturalists displaced from other regions (i.e. the “shifted cultivators”: Myers 1993), whose agricultural practices are often inappropriate and unsustainable in tropical forests; (3) they have broad ecosystem effects, including (i) causing environmental contamination by chemical pollutants (ii) causing noise disturbance (iii) altering habitat characteristics through increased edge exposure and (iv) increasing soil erosion and sediment runoff (Coffin, 2007) which impact aquatic species (Furniss *et al*., 1991) ; (3) they are a direct and significant source of animal mortality or “roadkill” (Coffin, 2007) and are avoided by many species, causing barriers to animal dispersal and population connectivity (Forman and Alexander, 1998); and (4) tropical forest species, most of which are preadapted to shaded, humid environments, are especially strongly impacted by linear clearings, which alter the local microclimate and create dispersal barriers for even mobile species (Laurance *et al*., 2009); and

Addressing poverty is a global priority enshrined in the United Nations Millennium Development Goals (UN MDG Report, 2015). This need is particularly acute in the tropics, whose residents are amongst the monetarily poorest people globally (Sachs *et al*., 2001). Infrastructure development, including road building, undoubtedly has the potential to increase market connectivity and generate income (Ogan, 2010). Advocates of biodiversity conservation are often criticised for proposing measures, including extensive habitat protection, which reduce the scope for infrastructural and agricultural development, thereby harming the poor (Nolte *et al*., 2013). Our study, which links urban areas, roads and other infrastructure to anthropogenic forest disturbance, may be seen in this light insofar as it echoes the findings and conundrums raised by other studies (Wilkie *et al*., 2000).

Legally occupied protected areas, including indigenous, extractive and sustainable-use forest reserves, although not a magic bullet, are part of the solution. As already noted, rural Amazonians are far poorer than their urban counterparts, a trend which is mirrored globally (Chen and Ravallion, 2007). Ill-conceived infrastructure development such as the Balbina hydroelectric dam (Fearnside, 1989) often generates income for urban elites whilst dispossessing relatively powerless forest dwellers (Watts, 2005). Sustainable use and other inhabited reserves therefore potentially protect both forests and their inhabitants.

Our study suggests that the rapid expansion of urban areas, road networks and other capital-intensive infrastructure is at least as relevant to biodiversity conservation as the trajectory of traditional *ribeirinho* populations in the Brazilian Amazon. Increased connectivity, access to market and opportunity for external actors to colonise, deforest and extract forest resources, may create “nodes” which will eventually become towns in their own right and transform these rivers from cul-de-sacs to bead chains, as has already happened in much of Pará.

Likewise, hunted areas are predicated on both the settlement pattern of rural households and the infrastructure that paves the way to colonisation of headwater regions. The more dispersed households are, the less overlap between their hunting catchments and the greater the area subject to hunting disturbance. Pseudo-interference ensures that more aggregated rural households impart less per capita disturbance, thereby leaving larger areas beyond easy access. Unless Brazilian government social welfare programs continue to sustain rural Amazonian populations, ongoing rural exodus may reduce hunting and other extractive practices that may or may not be sustainable. Conversely, the dwindling number of remote rural households may be insufficient to justify the maintenance and expansion of sustainable-use reserves, which can deter not only commercial hunters harvesting large amounts of game, but other external commercial enterprises that can catalyse large-scale deforestation.

Our study could be expanded upon and developed by (1) tracing the evolution of anthropogenic disturbance along rivers as they progress from virtually uninhabited, to cul-de-sac, to road-intersected, and finally to a bead-chain pattern. This would provide more insight into the possible trajectory of as yet largely undisturbed Amazonian rivers; (2) performing a structured nonparametric regression, for example a path analysis (see Appendix J). This would explicitly account for the structured nature of the causal interactions in this system.

2.5 Conclusions

This analysis lead us to reassess our notions of what motivates rural Amazonians in their settlement choices and their role in different scales of anthropogenic forest disturbance. Rural populations are often held accountable for much habitat and biodiversity loss in tropical forests (Schwartzman, *et al*., 2000) but incur disproportionately high costs associated with biodiversity conservation (Balmford and Whitten, 2003). These populations, however, are not homogenous, and include both agrarian settlers taking advantage of new development frontiers, as well as long-established extractivist communities, whose occupation of riparian corridors can buffer against the encroachment of more predatory agents of resource exploitation and land-use change.

Much of the Brazilian Amazon retains vast tracts of forest that are only accessible by river, which remain viable biodiversity refugia. Nations and states with sovereignty over the Earth’s remaining intact tropical forests are faced with alternative development trajectories. The needs of their citizenry, as well as the apparent imperative of economic growth and the lure of mega-projects and lucrative investment deals, may impel them to engage in large-scale road-building and other infrastructure development. Our analysis shows that, as accessibility is an overwhelmingly important mediator of forest disturbance, that trajectory culminates in a landscape dominated by road-intersected bead-chain rivers, within which forests are gradually eroded and degraded.

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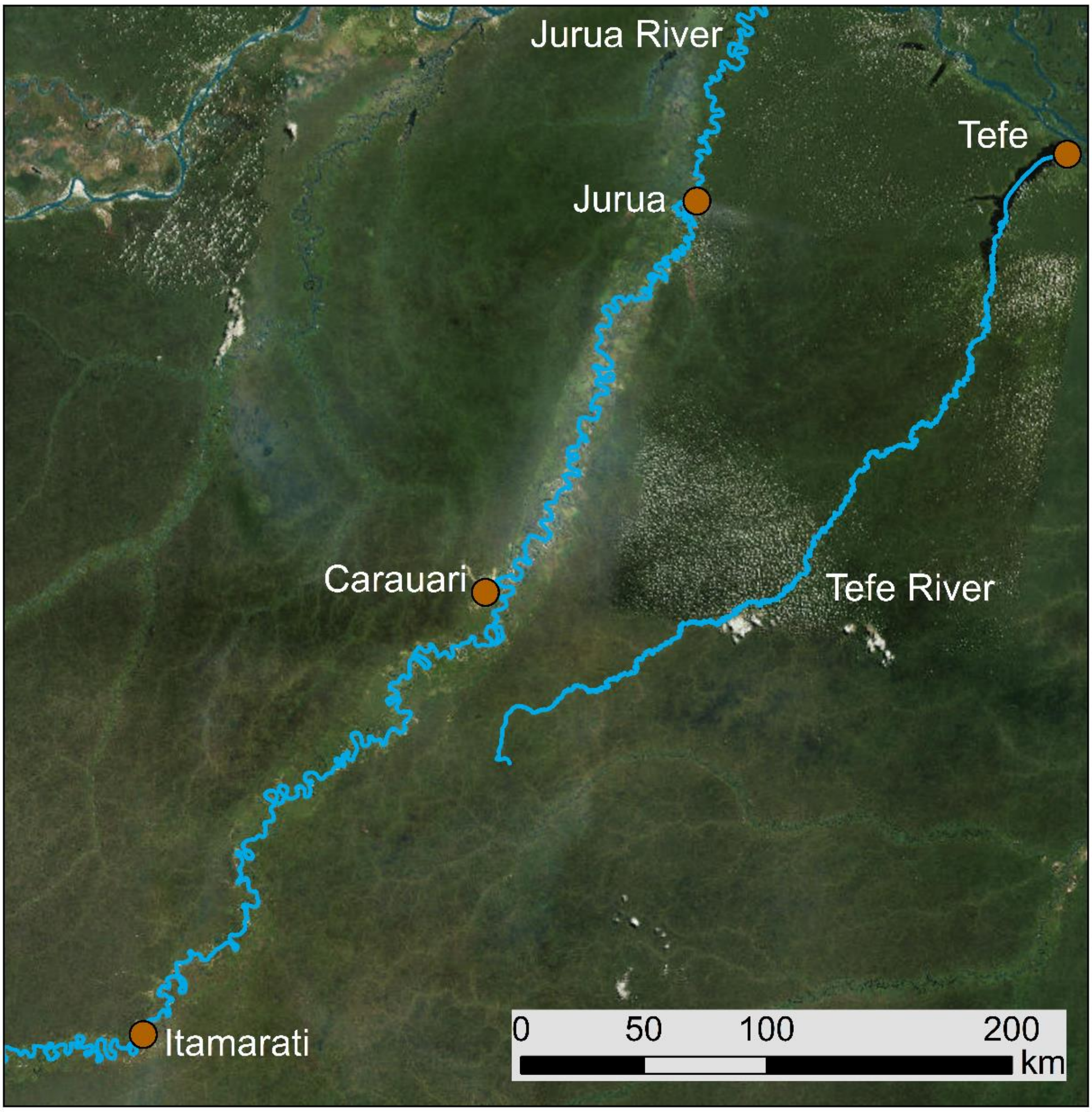
Appendices

APPENDIX A: Cul-de-sac and bead-chain rivers

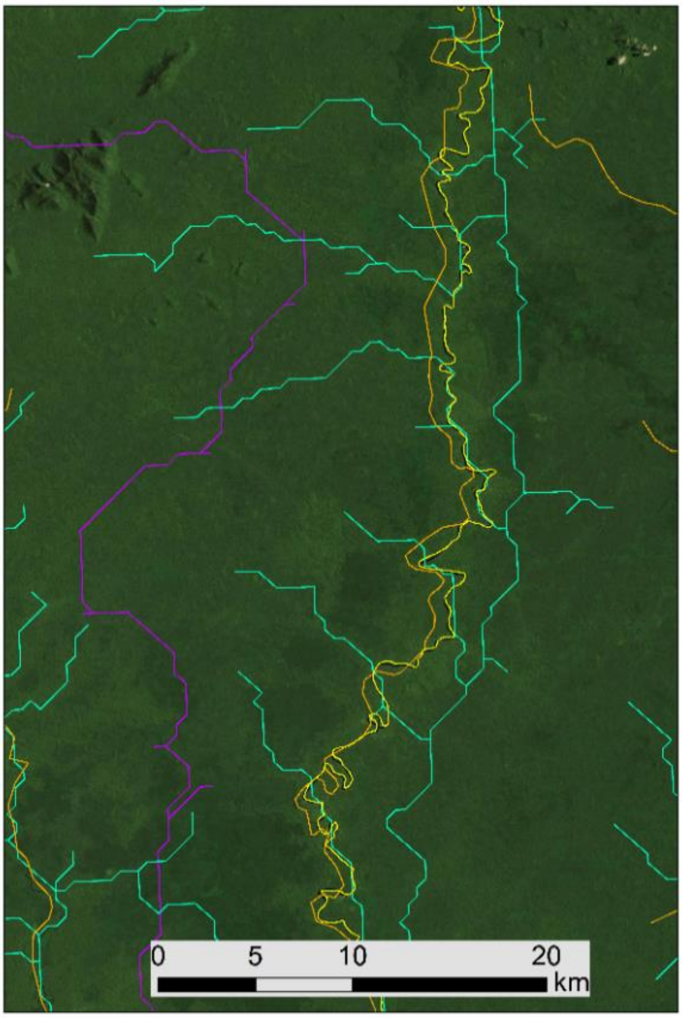
The map below shows the Juruá and Tefé rivers. The Juruá is a bead-chain river, with towns interspersed along its length. Inhabitants are influenced by inter-urban traffic as well as their nearest town. The Tefé is a cul-de-sac river, with a town at its mouth and therefore market influence is unipolar.



Though we anticipated that analysed rivers in the state of Para would be more deforested than those in Amazonas, this was not the case. This is likely due to the selection criteria in our methodology. We deliberately chose cul-de-sac rivers. These rivers by their nature, have lower levels of disturbance than bead-chain rivers. We were only able to identify 8 such rivers in the state of Para, whilst we identified 37 in the state of Amazonas. This disparity is partially explained by the difference in area between these states (Para is 80% as large as Amazonas) and their different fluvial geographies, but also by the fact that a larger proportion of rivers in Para have become bead-chains due to the expansion of road networks and towns.

APPENDIX B: River digitisation

The map below shows the Marauia River overlaid with the three existing river polyline shapefiles and the yellow digitised line. The IBGE “hidro tot linha” (HTL) shapefile, represented by an orange line is faithful to the overall geometry of rivers, but generally simplified and with greater inaccuracies for smaller rivers. The Hydrosheds hydrographic dataset from Lehner and Grill, 2013, represented by a blue line, is generally accurate, but with occasional very large path errors. The Amazon River Basin Land and Stream Drainage Direction ORNL DAAC Maps from Mayorga *et al*., 2012, represented by a purple line, was found to be consistently the least accurate. These inaccuracies are generally not detrimental to large-scale studies, especially those focussing on first order tributaries of the Amazon/Solimoes.



The complex fluvial geometry and seasonal inundation of the Amazon basin makes definitive river digitisation challenging. To make a fine-scale fluvial map over such a vast area, the use of basemaps of inconsistent resolution and timeframe is a necessary compromise, mitigated by the application of consistent methodological rules.

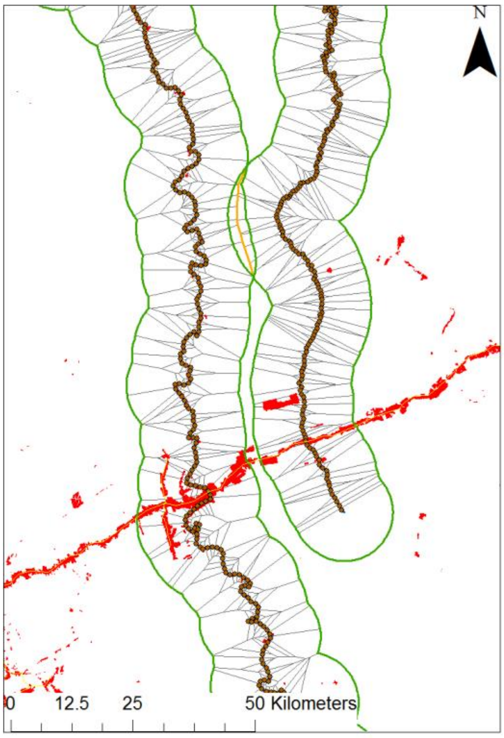
Consistent digitisation rules were applied as follows. The river “mouth” was taken to be where the river meets a town or a bead-chain river. Rivers were digitised into the remote headwaters until it was no longer possible to make out the course of the river. The most extensively and densely populated river channel was digitised. Subject to the above constraint, the shortest route was digitised, avoiding for example, uninhabited anabranches. This simulates how inhabitants travel to market towns. For wide rivers, the midpoint was digitised. Large obstructions such as islands were digitised around.

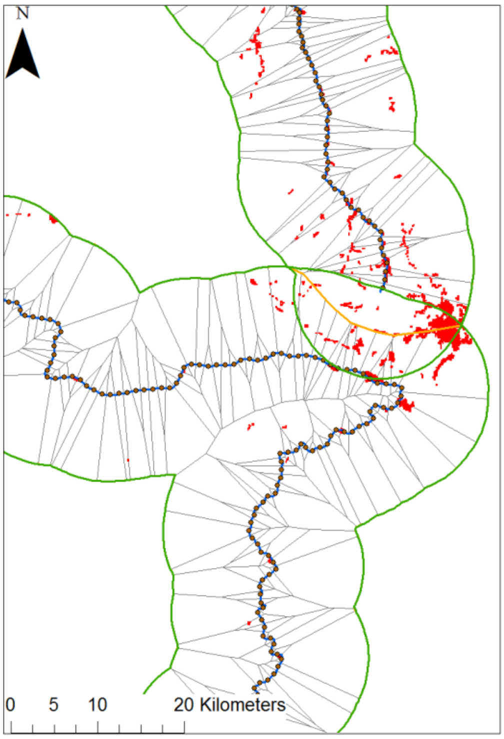
In order to determine the degree to which the aforementioned river shapefiles are suitable for analyses of anthropogenic disturbance, the HTL shapefile was validated against the digitised rivers as follows. The HTL rivers corresponding to those that had been digitised were selected and checked to ensure that the entire river paths were represented, from the headwaters to the mouths. The HTL rivers were truncated where they met an urban area or bead-chain river, as per the digitised rivers, but they were not truncated in their headwaters, even if these extended beyond those of the digitised rivers. In order to restrict HTL rivers to single lines, side-tributaries and lakes were removed, and where both banks were represented, the bank corresponding most closely to the digitised river, was chosen. Buffers of 10km were created around the HTL and digitised rivers. Per river, using both HTL and digitised shapefiles, the non-linear fluvial length and the number of rural households and area of deforestation within the buffers were calculated. These were subsequently compared using Spearman’s Rank correlation tests. Additionally, per river, the degree of overlap between the buffers of the HTL and digitised rivers was calculated.

On average, the HTL rivers were 81% (± 2%) as long (non-linear fluvial distance) as the digitised rivers, reflecting their simplification of small-scale river sinuosity. Despite this, mean proportional overlap between the HTL and digitised river buffers was extremely high (0.92 ± 0.01). Likewise, the nonparametric correlation between river length, number of rural households and area of deforestation between the HTL and digitised rivers was extremely high (Spearman’s Rho > 0.95 in all cases). Although we opted to use the more accurate, digitised river shapefiles, we anticipate that the HTL shapefile, suitably adapted, would produce similar results and require a far lower input of digitisation labour.

APPENDIX C: Data Partitioning Using Thiessen Polygons

The maps below demonstrate how data were partitioned between rivers to avoid double-counting. Segments of two example rivers are shown as blue lines. 10km buffers around the rivers are shown in green. Deforested area to be partitioned between rivers is shown in red. Brown dots represent the midpoints of 1km fluvial segments along the rivers. Thin black lines (clipped by the buffer boundary) represent the thiessen polygons around the 1km points. The orange line is the thiessen-derived interface between the two rivers.





APPENDIX D: Cross-validation of households and deforestation datasets

The table below compares the PRODES raster datasets between 2007 and 2013. The 2009 dataset was chosen because it has the smallest area of cloud and no-data and the largest area of data. It also corresponds closely in time to the 2007-2009 households census.

Yr	**no data cells**	**data cells**	**cloud cells**	**cell size m**	**area per cell m^2**	**no data km^2**	**data km^2**	**cloud km^2**
2013	516596930	555917128	80109142	90	8100	4184435	4502929	648884
2012	476386530	596127528	38370048	90	8100	3858731	4828633	310797
2011	475120657	598433411	36681641	90	8100	3848477	4847311	297121
2010	492497080	581056988	54072551	90	8100	3989226	4706562	437988
2009	262026591	341073034	15757106	120	14400	3773183	4911452	226902
2008	271926486	328258890	15962705	120	14400	3915741	4726928	229863
2007	279069068	321827326	20524032	120	14400	4018595	4634313	295546

The rural households points shapefile was aggregated at the level of census sector and district for the states of Amazonas, Para, Acre, Mato Grosso, Rondônia and Roraima, so that it could be compared to the IBGE 2007 rural population count. Similarly, the 2009 PRODES deforestation data was compared to the Hansen *et al.*, 2013 Global Forest Loss (GFL) dataset. The GFL "Year of gross forest cover loss event" raster layer was used so that loss until 2009 could be compared. In both cases, cells were reclassified into either deforested or not deforested. A subset of data for which there was both PRODES and GFL data was taken from the 00N_070W degree granule in the state of Amazonas. The data were aligned and aggregated (using ArcGIS tools "extract by mask" and "aggregate") to a cell size of roughly 12500m, representing a 100 cell factor aggregation of the PRODES dataset. A 30km buffer was erased from this area to exclude edge effects caused by raster aggregation, leaving an area of analysis of 1,072,620 km^2.

For both deforestation and households, a Spearman's rank test was performed. The rural households point shapefile and the IBGE 2007 rural population census, were found to be strongly correlated. Aggregated by census sector, N = 8314, Spearman's Rho = 0.69. Aggregated by district, N = 721, Spearman's Rho = 0.85. Likewise, the 2009 PRODES dataset was found to be strongly correlated to the GFL dataset N = 6854. Spearman's Rho = 0.71.

Note that the GFL data is at a finer, 30m resolution and does not appear to have cloud. It classifies pixels as percent deforested. It classifies any vegetation above 5m in height as forest. It does not classify natural non-forest.

APPENDIX E: Urban proximity score

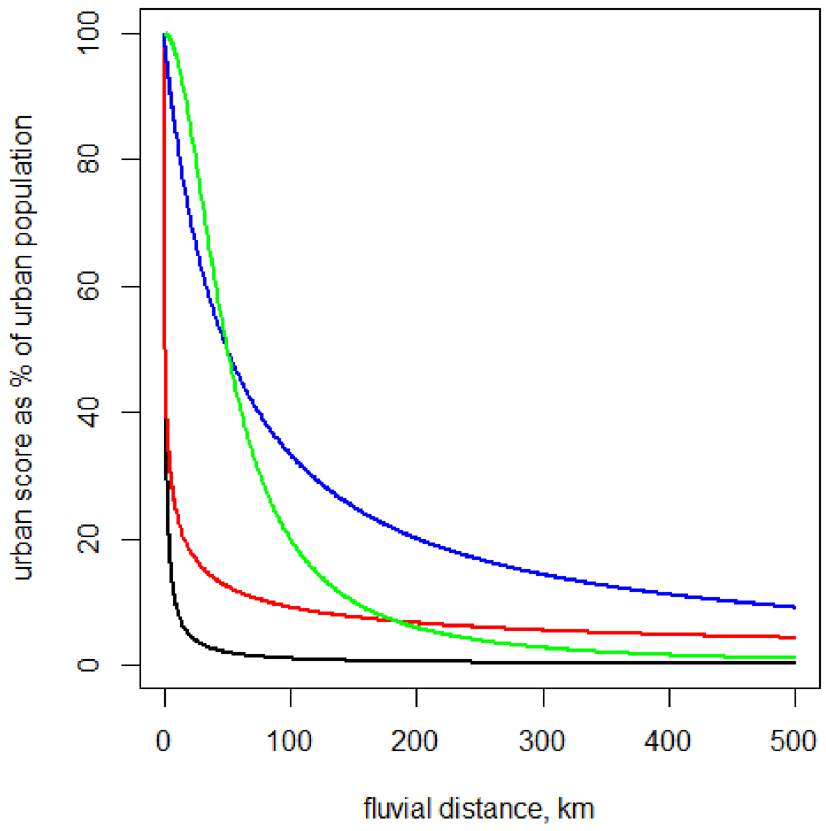
We sought a variable that captures, in a way relevant to the forces acting on rural Amazonians, the degree to which a given river has access to urban centres. Urban population size determines numerous important factors including the size of the market for agricultural produce and the accessibility and cost of essential services and industrially produced goods. For an urban centre of a given population, increased travel cost limits its utility to a rural Amazonian. Therefore we moderated the urban population by travel cost. Data for urban populations was taken from the IBGE 2010 census, as this had more accurate associated census sector shapefiles than the 2007-2009 data. Urban permanent private households per census sector were summed per town. To avoid including small urban aggregations with limited market for rural goods or provision of important services, towns with fewer than 1000 households were excluded. For each target river, the fluvial distance between the river mouth and every town was calculated using Network Analyst in ArcGIS. Fluvial distance was converted to travel days, taken to be 50 fluvial km for a rural Amazonian using a canoe and small outboard motor (locally *rabeta*), as confirmed by our field experience. We then created an urban proximity index which moderates the urban population by the travel cost, by dividing the number of urban households in a given town by one plus the number of days travel to the river mouth. Thus a town at a distance of zero fluvial km from the mouth of a target river would contribute a score equal to the number of its urban households, whilst a town exactly 50 fluvial km (one travel day) away would contribute half that number. The scores for the two nearest towns per river were summed to give the overall score per river.

We consider this variable to provide a relevant metric of urban accessibility, but we recognise that its formulation may appear *ad hoc*. When creating the index, we did not do so with the explicit aim of maximising the correlation with deforestation or population density. We chose this index because it has the following advantages. (1) Excluding towns with fewer than 1000 households is important as they provide limited goods, services or market for agricultural produce. (2) Summing the score for the two closest towns accounts for rivers which, although not very close to a large town, are fairly close to two large towns. (3) Travel days are a meaningful unit of travel cost. (4) Because one was added to the denominator, at a distance of zero, the urban score is equal to the urban population. The score never exceeds the urban population (5) the score is useable for distances between zero and one. It is always positive and decreases with distance.

Other indices that have similar properties, but were not chosen are (1) Urban.dist, calculated by dividing the number of urban households by the fluvial distance plus one. This severely reduces the urban score for rivers more than 1km from a town. The score is reduced to 3.8% in only 25 fluvial km from a town. (2) Urban.sqrt, calculated by dividing the number of urban households by the square root of the fluvial distance, then adding one. Alternatives which replaced the square root with the cube and fourth root were also tested. For distances greater than 1km these indices are less severe than the above, but at distances between 0 and 1km, they are more severe. The square root still reduces the town score to 16.7% in 25 km. The negative exponent is still too steep initially and becomes shallow too soon. (3) Urban.sq, calculated by dividing the number of urban households by the square of the travel days, then adding one. This index also has desirable properties, but is no less ad hoc than the original index.

The graph below shows the relationship between the urban score as a percentage of the urban population of a hypothetical town and the fluvial distance from the river mouth. The black, red, green and blue lines represent Urban.dist, Urban.sqrt, the original urban index and Urban.sq respectively.

In the Spearman’s correlation matrix we created (a) all four indices are highly correlated (Spearman’s Rho > 0.82 in all cases) and (b) the index we chose to use has the lowest pairwise nonparametric correlation with both deforestation and households (Spearman’s Rho = 0.63 and 0.37 respectively) out of all the indices. Therefore we are confident that any suitably created urban index would be equally if not more influential in GLMs.

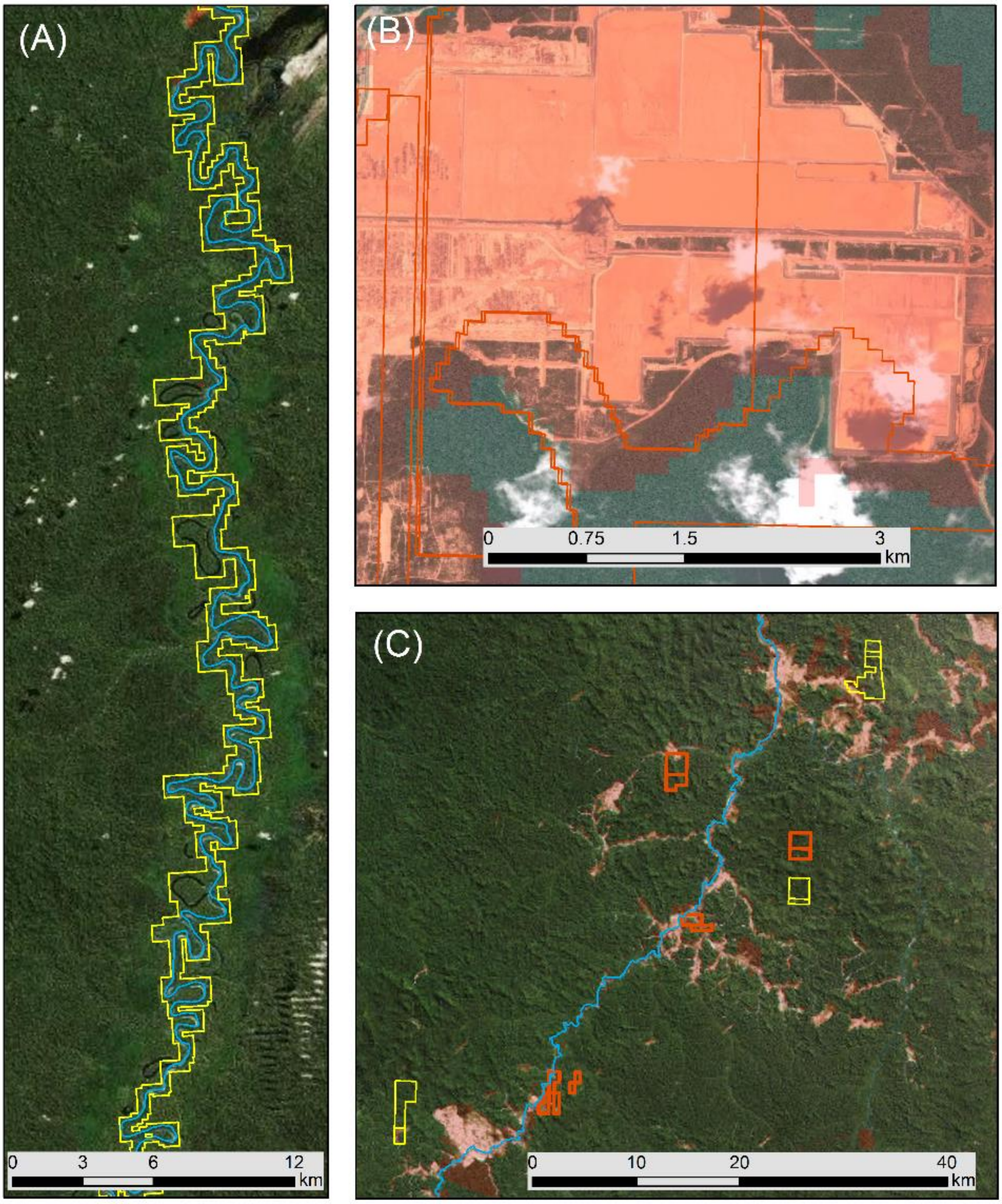


APPENDIX F: Mines

Mines are often associated with a characteristic extensive deforestation pattern that is visually distinct from agricultural fields and cattle pasture. Upon inspection, there appeared to be large areas of mining activity with no associated registered mines (commercial or artisanal). Furthermore, the artisanal mines polygons did not correspond reliably to visually obvious mines. This may be because the mining shapefiles are outdated, or because of unregistered mines. It was decided to use the registered commercial and artisanal mines shapefiles and not to digitise areas of apparent mining. It would be fallacious to model deforestation using a variable based on visually apparent widespread deforestation at the expense of officially recognised mines.

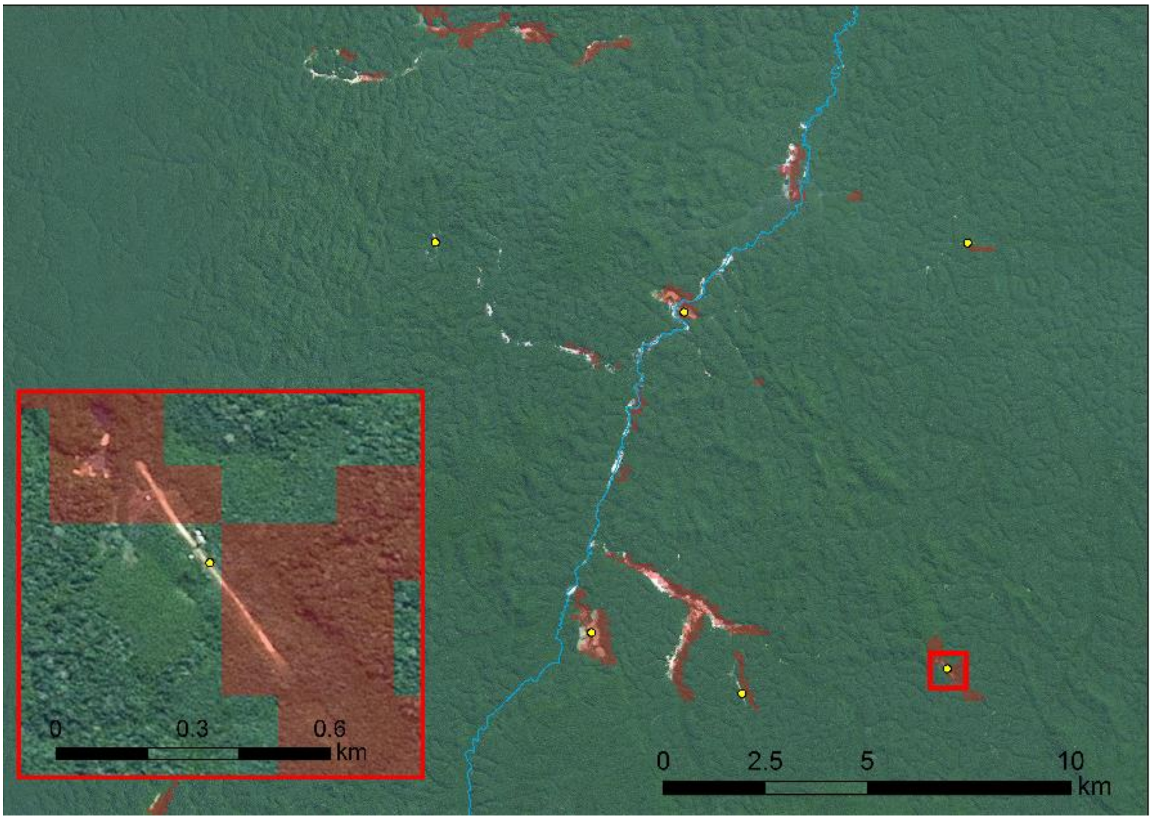
Artisanal mines were not retained in any of our models and commercial mines were not retained in deforestation models. This may be because polygons of registered mines do not accurately capture de facto mining operations and our definition of disturbance does not include undoubtedly important aquatic and soil pollution for which mines are notorious (Malm, 1998), but which are virtually undetectable from satellite images. In lieu of a more holistic analysis of disturbance, ground-truthed or otherwise independently verified maps of mining operations would likely be stronger predictors of deforestation.

The three examples below show areas of registered mining. The background is an ESRI basemap. Brown outlined polygons indicate areas of registered commercial mines and yellow outlined polygons indicate registered artisanal mines. Pixels classified as deforested by PRODES 2009 are transparent red polygons. Panel A shows a stretch of river (Jandiatuba) with a large area of registered artisanal mining but no associated deforestation. Panel B shows a large registered commercial mine. Panel C shows an area in which areas of deforestation, presumably due to mining, do not correspond closely to areas of nearby registered commercial or artisanal mining.


(A)
0
3
6
12
km
(B)
0
0.75
1.5
3
km
(C)
0
10
20
40
km

APPENDIX G: Airstrips

The map below shows a set of rural airstrips adjacent to the Maues-Amana river (blue line). The background is an ESRI basemap. Yellow dots indicate the centre of the airstrip. Red transparent polygons indicate pixels classified in PRODES 2009 as deforestation. The red outlined polygon is an inset for clarity. Airstrips are easily identifiable from ESRI basemaps. In this case, they appear to be associated with an area of unregistered mines.



APPENDIX H: River Chemistry

Rivers were initially categorised as either whitewater, blackwater or clear-water, a classification dating back to Alfred Russel Wallace (Wallace, 1853 and Sioli, 1950). The main data source used was Junk *et al.*, 2015. This was supplemented by Goulding *et al.*, 2003 “The Smithsonian Atlas of the Amazon” and the Radar na Amazônia (RADAMBRASIL) vegetation classification. Rivers not covered by these sources were estimated by eye. Because many of the rivers are small and relatively unknown, reliable river chemistry data was scarce and confidence in the meaningfulness of the resulting classification was low. Therefore it was decided to use soil fertility instead of river chemistry, which was excluded from the analysis.

APPENDIX I: Exposure variables

An assumption of our households and deforestation models, is that the area associated with a given river acts as an exposure variable. Rivers with a larger associated area have a larger deforestation potential and therefore raw deforestation per river are not directly comparable. There appears however to be a positive relationship (Fig. 2.2) between the associated area per river and the percentage of that area which is undisturbed. This suggests that for cul-de-sac rivers, disturbance is somewhat constrained and does not increase linearly with available area. Given the importance of access to urban centres, this may reflect the prohibitive cost of travelling far up our studied rivers. Spearman's correlation tests however reveal that the relationship between associated area and undisturbed percentage, household density and deforested percentage are relatively weak (Spearman's Rho = 0.38, -0.17 and -0.34 respectively). Therefore we feel justified in using the associated area as an offset variable in models.

APPENDIX J: Structured equation model

Due to the interlinkages between variables in this analysis, a structured equation model using the “sem” function of the “lavaan” R package was created. We hoped to thereby simultaneously account for causal interrelations between variables and determine their relative importance in explaining deforestation. A Spearman's covariance matrix was used. The structure of the model was fourfold (1) deforestation was assumed to be directly dependent upon the number of rural households, the urban score and the remaining anthropogenic variables (mines, airstrips, roads, protected area) (2) rural households were assumed to be directly dependent upon the urban score and the remaining anthropogenic and environmental variables (river width, length, fertility and navigability) (3) the urban score was assumed to be directly dependent upon environmental variables (4) rural airstrips and mines were assumed to covary. There are a plethora of methods for evaluating the overall fit of structural equation models (Hooper *et al.*, 2008). Although we attempted several simplifications and variations on the above model specification, we could not specify a model that simultaneously met the criteria for Root Mean Square Error of Approximation, Comparative Fit Index and Tucker-Lewis Index. Therefore we do not report these models here and instead report the GLMs created to separately analyse deforestation and rural population density.

APPENDIX K: Theorised drivers of disturbance

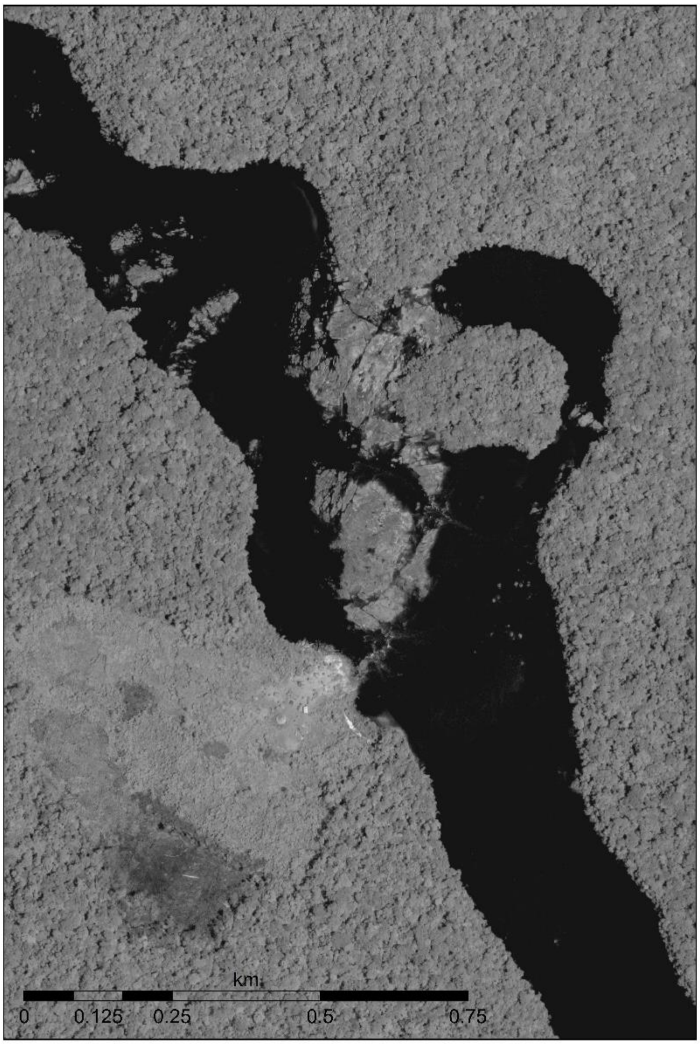
Overall soil fertility, and associated patterns of rainfall and fluvial geochemistry, influence both agricultural productivity and the availability of wild game and fish (Janzen, 1974, Coomes, 1998). Rainfall and drainage geometry also affect the viability of road construction (Kabila *et al*., 2009). Fluvial navigability, as predicted by river slope and the prevalence of rapids and waterfalls, influences travel costs in terms of time and fluvial transport risks. Rivers in roadless regions of lowland tropical forest are the only viable means of travel between most rural households and urban centers. Poor navigability increases the cost of acquiring essential goods and services (Parry *et al*., 2010a).

River size, as measured by length, width, and discharge, also influences disturbance. The largest Amazonian towns, such as Belém and Manaus, border the largest rivers, because they are the trade highways linking sources of natural resources to markets. In addition, longer rivers have correspondingly larger accessible areas to both deforest and hunt (but see Appendix I).

Anthropogenic factors such as mineral deposits can directly fuel deforestation and potentially increase human population density through employment provision. Airports and airstrips bypass fluvial navigability constraints, allowing for rapid, but expensive transport. Their presence indicates the influence of external actors with access to capital. Roads provide an alternative to fluvial transport. They allow local communities greater access to markets and greater access by outsiders to natural resources. Legally protected areas restrict settlement and disturbance activities, although legally inhabited sustainable-use reserves and indigenous territories, contain many semi-subsistence communities. Lastly, rivers near larger urban centers are more attractive to rural households, especially agricultural producers, and therefore more prone to direct disturbance.

APPENDIX L: Supplementing unrecorded waterfalls and major rapids

The image below shows an example of an area where turbulent rapids and/or waterfalls make fluvial navigation challenging. The example below, along the Mapuera River, was not recorded in available waterfalls datasets, but was uncovered through visual assessment of ESRI Basemaps.



APPENDIX M: Protected areas

We assume that protected status is causally responsible for lower human population density and disturbance, rather than the reverse. Additionally, due to overlapping protected areas, we did not distinguish between the different types of protected area. In our vast study landscape, protection is logistically difficult to enforce, raising the concern that these may be “paper parks” (Bruner *et al.,* 2001). Also, there is lower resistance to protection in areas of marginal economic value and low human population density (Andam *et al.,* 2008 and Mas, 2004). It is therefore plausible that human population density and disturbance deter protection as much as the reverse. Nonetheless there is strong evidence (Nolte *et al.,* 2002, Nepstad *et al.,* 2006) that protected areas including inhabited reserves significantly inhibit disturbance including deforestation and fire.

APPENDIX N: Hunted area

Existing hunting studies use interviews, transects and hunt follows to create detailed assessments of hunting catchments in localised areas (Parry and Peres, 2015, Peres, 2000, De Souza-Mazurek *et al.*, 2000), or use roads and rivers to calculate areas accessible to hunters (Peres and Lake, 2003). This study by contrast, uses spatially explicit households data to deduce hunted area on a large scale. Hunting pressure is notoriously difficult to quantify (Robinson and Bennet, 2013). It would be impossible to do so directly at this scale. Thus we employ a simple measure of accessibility by hunters, based on widely supported literature values for hunt distance. This ignores small-scale landscape features, regional and cultural differences in hunting practices and differences in hunting intensity.

APPENDIX O: Unhunted deforested area

Though the unhunted deforested area was small in absolute terms as expected, it surprisingly represented 10.5% of the deforested area. It is unlikely that this area is due to active small-scale agricultural plots distant from corresponding rural households. It is likely to be a combination of past deforestation caused by rural households that have since relocated, deforestation caused by unregistered rural households, pixels misclassified by PRODES and deforestation caused by nonresidents, for example unregistered mines and cattle ranches.

Chapter 3: Semi-subsistence Amazonians incur significant agricultural losses to forest vertebrate crop raiders

Submitted to The Journal of Wildlife Management as:

Abrahams, M.I., Costa, H.C.M., and Peres, C.A. Semi-Subsistence Agricultural Losses to Forest Vertebrate Crop Raiders in Amazonia

Abstract

Tropical megadiversity benefits humanity, but the high costs of coexisting with biodiversity disincentivize local communities from conserving it. Here, we harness social and ecological approaches to quantify, contextualise and explain the prevalence of terrestrial vertebrate crop raiding damage to manioc (*Manihot esculenta*) agricultural plots in the Medio-Jurua region of western Brazilian Amazonia. A total of 132 camera trap stations and 157 quantitative interviews were deployed across the peri-community areas controlled by 47 semi-subsistence communities. Across 238 plots, mean reported loss to crop raiders was 7.33 ± 0.98%. However, interviewees estimated counterfactual losses of 73.93 ± 2.98% per annum in the absence of crop protection from crop-raider suppression. Species reported to enter manioc plots were frequently detected by camera traps, particularly in early-successional forest habitats. Generalised Linear Mixed-Effects Models indicate that human population pressure depresses both reported crop raiding losses and camera-detected crop raider biomass. Nonetheless there was weak evidence that opportunities to hunt crop raiders compensate crop losses. Our study indicates that vertebrate crop raiders represent a significant forest ecosystem disservice, incurring livelihood costs through immediate crop losses, constrained crop choice, and effort allocated to crop protection. Small communities far from urban centers, who are already economically disadvantaged, were worst affected.

3.1 Introduction

Semi-subsistence rural communities in the tropics are amongst the world's monetarily poorest people (Sachs *et al*., 2001) but often live in the world's most biodiverse places (Gaston, 2000). They are frequently exhorted by the international conservation community to protect their megadiverse surroundings (Mittermeier *et al*., 1998). However, living with and protecting natural ecosystems and their biodiversity can incur significant local costs, whilst the benefits may accrue internationally (Balmford and Whitten, 2003). Crop raiding is an ecosystem disservice (Zhang *et al*., 2007) straining already precarious livelihoods through decreased crop yields (Hill, 2000; Gillingham and Lee, 2003) and the labour required to protect crops. The international conservation community must recognise these socioeconomic costs when extolling tropical forest dwellers to coexist with and preserve biodiversity.

Crop raiding has received considerable attention in the Afrotropics and Asian Tropics (Sukumar, 1990; Naughton-Treves, 1998; Pienkowski *et al*., 1998; Hill, 2000; Linkie *et al*., 2007), where crops including manioc (*Manihot esculenta*), maize (*Zea mays*), Japanese radish (*Raphanus sativus*), Asian rice (*Oryza sativa*) and finger millet (*Eleusine coracana*) are raided by large-bodied mammals including chimpanzee (*Pan troglodytes*), olive baboon (*Papio hamadryas anubis*), Japanese macaque (*Macaca fuscata*), wild boar *(Sus scrofa*), pig-tailed macaque (*Macaca nemestrina*), Asian elephant (*Elephas maximus*) and African elephant (*Loxodonta africana*). Hill (2000) and Naughton-Treves (1998) estimated manioc crop losses of 9.0% (overall) and 6.8 ± 2.1%, respectively, in Uganda, whilst Nchanji (2002) estimated manioc losses of 2.4% - 15.1% in Cameroon. These losses have been shown to negatively impact local attitudes to conservation and protected areas (Hill, 2000; Nyhus and Sumianto, 2000; Gillingham and Lee, 2003; Wang *et al.,* 2006; Mackenzie and Ahabyona, 2012). Reported farmer responses to crop raiders include farm abandonment, leaving some land fallow, building fences, guarding and patrolling fields, overnight vigils, and deploying snares, traps, poison bait, guard dogs, guard huts, guns, spears, bow-and-arrows, fireworks, noisemakers and bells to chase or otherwise scare away undesirable animals (Naughton-Treves, 1998; Hill, 2000; Gillingham and Lee, 2003; Linkie *et al*., 2007).

Description and quantification of crop raiding in the Neotropics is at best limited (Estrada, 2006). Naughton-Treves *et al.* (2003) found that hunting intensity had a greater impact on mammals in Tambopata, southern Peru, than swidden agriculture and that whilst crop losses were higher in remote areas, they were compensated by higher game meat harvest. Pérez and Pacheco (2006) report ~16% losses to crop raiders across three crop types in their Bolivian study.

The interaction between crop raiders and communities requires integrated socio-ecological approaches which are still rare. Studies have used sampling methods ranging from interviews (Hill, 2000), experimental plots (Pérez and Pacheco, 2006), sign surveys (Naughton-Treves,

1998) and camera traps (Krief *et al., 2014).* Interviews distil decades of local knowledge and are relatively inexpensive to deploy, but their reliability can be questioned, especially given the sensitive nature of the topic (Tourangeau and Smith, 1996; Gavin *et al*., 2010). Camera traps are increasingly used for biodiversity surveys (Rowcliffe and Carbone, 2008). They have proved reliable compared to other survey methods (Benchimol and Peres, 2015). However, they only provide a spatio-temporal snapshot, and are expensive, prone to fail in the tropics, are stolen and when used to produce relative abundance estimates, may be unreliable when there are significant habitat-induced detectability biases (Sollmann, 2013). Interviews and camera traps may therefore complement one another.

Manioc is the staple source of carbohydrates in Brazilian Amazonia and in much of the humid tropics where nutrient-poor soils have high levels of aluminium toxicity (Cock, 1982; Frazer, 2010). Crops including maize and bananas are also locally important, and have their own attendant crop raiders, but their higher nutrient requirements prevent their large scale cultivation in most of Amazonia. The main varieties of manioc are high-cyanide manioc (Peroni *et al*., 2007), locally called "*roça brava*", and low-cyanide manioc, locally called "*macaxeira*" (hereafter, *bitter manioc* and *sweet manioc,* respectively). *M. esculenta* produces large tubers, tolerates poor tropical soils and is pest-resistant. Manioc is processed in a flour-house (locally "*casa de farinha*") into a relatively imperishable, high calorie course flour (locally "*farinha*"). Communities grow manioc in swidden agricultural plots called *roçados,* often representing the main livelihood activity for semi-subsistence riparian communities in the lowland Amazon (Newton *et al*., 2012) *Roçados* are generally active for 4 years until weed encroachment and declining soil fertility force their abandonment (Unruh, 1988). These secondary forests (locally "*capoeiras*") are left to undergo successional regrowth until standing biomass and soil nutrient loads are sufficient to permit re-clearing. This process creates a mosaic of habitats under different successional stages around village settlements, with shorter-rotation plots generally closer to the community (Coomes *et al.,* 2000).

We anticipate that the highest rates of reported losses to crop raiders and the highest crop raider biomass will be recorded farther from the community, surrounded by more undisturbed habitat, at smaller communities, farther from large urban centers and closer to seasonally flooded forest (hereafter, *várzea*). *Roçados* farther from a given community are more likely to be raided because they are harder to protect and experience lower hunting pressure (Smith, 2008). Primary forest areas beyond successional mosaics consolidated around settlements provide a reservoir of crop raiders (Hartter *et al.,* 2010). These species, although tolerant of disturbed areas and attracted by crops, rely on primary forest (Barlow *et al.,* 2007). Thus *roçados* adjacent to contiguous primary forest are more accessible to raiders (Naughton-Treves, 1998; Hill, 2000). *Roçados* farther from the community are also more likely to be adjacent to contiguous primary forest. Larger communities exert higher hunting pressure (Alvard *et al.,* 1997), have a smaller proportion of *roçado* “edge” adjacent to primary forest, and are thereby likely to experience less raiding. *Roçados* near towns, or in peri-urban communities, will likely be less raided for similar reasons. Conversely, however, the larger a community, the more scarce land becomes near to the community centre. Thus farmers are likely to have *roçados* farther from the centre (Coomes *et al.*, 2000). In addition, vertebrate herbivores in more anthropogenic landscapes may crop raid more frequently due to the relative shortage of natural food (Yamada and Muroyama, 2010). *Várzea* soil is more fertile due to sediment and debris deposition. Ceteris paribus, productivity and crop raider biomass should to be higher in Amazonian *várzea* forests (Peres, 1997). As communities are often at the intersection between *várzea* and non-flooded terra firme forest (Junk, 1984), this effect may be masked by anthropogenic pressures. We anticipate that crop raiders are disproportionately targeted by hunters, and that farmers predominantly use lethal methods to suppress crop raiders, because crop raiders are likely to venture close to communities and killing them represents a ‘win-win’ strategy that both contributes wild meat to local households and reduces rates of crop raiding (Naughton-Treves *et al., 2003;* Smith, 2005; Gavin, 2007; Parry *et al.*, 2009).

Here, we used both structured local interviews and a camera-trapping sampling protocol to (1) quantify rates of terrestrial vertebrate crop raiding damage (hereafter, crop raiding) to manioc fields in western Brazilian Amazonia; (2) contextualise the importance of this damage in terms of livelihoods and local response strategies; (3) implicate the species that use *roçados* and those known to crop raid; (4) determine if those species are also important hunted species that are frequently detected by camera traps in the wider peri-community agricultural mosaic; and (5) using comparable explanatory variables and statistical techniques, determine the correlates of losses to crop raiders, crop raider and non-raider biomass, and the species composition of forest vertebrates. To our knowledge this is the first study combining camera trapping and interview data to understand crop raiding anywhere in the Neotropics.

3.2 Methods

3.2.1 Study Area

This study was carried out within and around the Uacari Sustainable Use Reserve (623,929 ha) and the Medio Jurua Extractive Reserve (250,192 ha) in the Medio Juruá region of western Brazilian Amazonia, which is bisected by the Jurua River, the second-largest white-water tributary of the Amazon (Fig. 3.1). These reserves are dominated by seasonally-flooded *várzea* forest (20 %) along extensive floodplains and unflooded (*terra firme*) forest on higher terrain (80 %). This region is inhabited by former rubber-tapper communities of mixed-descent semi-subsistence "*ribeirinhos*", with producer cooperatives and resource-management programs. The nearest towns are Carauari (88 fluvial km from the reserve boundary) and Itamarati (120 fluvial km from the reserve boundary), and provide vital access to goods and services (Parry *et al.*, 2010).

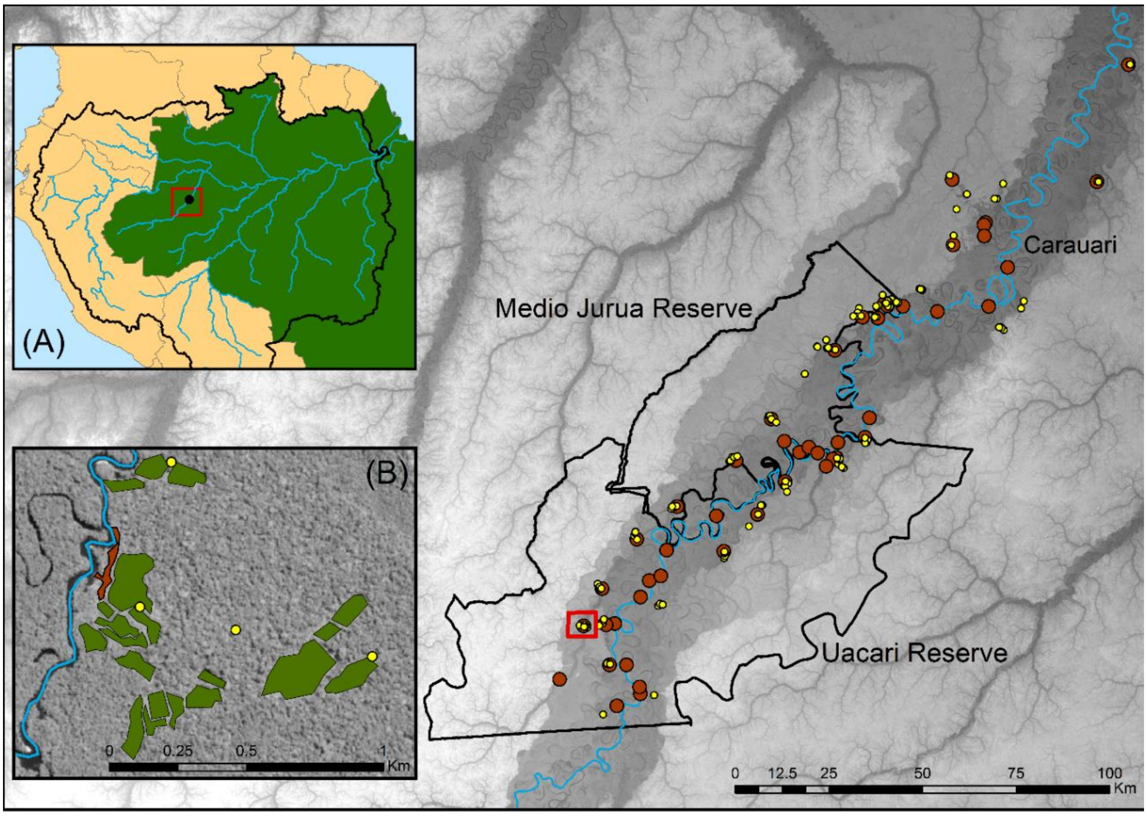


***Figure 3.1**: **Panel A** – Continental scale location of the study area, showing major rivers (blue lines) and the main urban center of Carauari (black dot). **Main Panel** (red square in Panel A**)** shows the Medio Jurua study region, where background represents elevation above sea level. Low elevation (dark grey) areas adjacent to the river represent seasonally-flooded (várzea) forests. Sustainable use reserves and the Jurua River are outlined in black and indicated by the blue line, respectively. Brown circles indicate the 47 surveyed communities/urban neighbourhoods, and yellow dots indicate the 132 camera-trap deployment sites. **Panel B** (red square in Main Panel) – An example of a surveyed local community, where household cluster area is delimited by a brown polygon; a tributary of the Jurua (Anaxiqui River) is indicated by a blue line; and the background is an ESRI basemap consisting largely of primary forest. Second-growth areas of mostly terra firme forests (capoeiras) and camera trap deployment sites are indicated by green polygons and yellow dots, respectively.*

3.2.2 Camera Trapping

Data collection took place between 2013 and 2015, generally between April and August avoiding the period of heaviest rain during which cameras are often damaged. A total of 132 camera-trap deployments were conducted according to a standardised deployment protocol (Appendix C1). Mean functioning camera-trap-nights (CTN) per deployment was 31.9 ± 0.5. Mean nearest neighbour distance between deployments was 974.4 ± 173.9 m, although camera-traps were deployed along a ~514-km nonlinear distance along the Juruá River. Deployments were stratified across several landscape-scale habitat types including: (1) large tracts of undisturbed primary contiguous forest; and anthropogenic successional mosaics in the vicinities of local communities, including (2) disturbed forest including small primary forest fragments, natural rubber tapping areas (*seringais*), degraded primary forest, and secondary forest older than 25 years; (3) secondary forest up to 25 years old; and (4) homestead areas in close proximity to community households. As per local requests, deployments were excluded from active manioc plantations (*roçados*) to avoid disturbing agricultural activity, although all landscape elements within successional mosaics were typically adjacent to *roçados*.

For each deployment, the following data were recorded: (1) the name and coordinates of the nearest local community; (2) coordinates of the camera-trap station; (3) date and time of deployment and removal; (4) in case of malfunction; date and time of last photograph; (5) habitat type; (6) if deployed in secondary forest, age since abandonment as determined by community residents.

Images were edited to improve contrast and aid species identification. Images per deployment were separated into subfolders corresponding to morphospecies. Images of domestic animals, humans, vultures, bats, insects, small lizards and primates were excluded from further analysis. We extracted all metadata from subfolders using software including the camtrapR package within R (Niedballa *et al.*, 2016) and Picture Information Extractor (Picmeta Systems, 2016). Images of conspecifics at any given deployment >30 min apart were defined as independent detections.

In the case of ambiguous images for which a subject could only be identified to a broader morphospecies, a deployment-specific detection ratio was calculated for each morphospecies sub-category. This ratio was used to apportion detections between sub-categories. If that deployment included no photographs that could be identified with certainty to either sub-category, then the overall detection ration for all deployments was used.

The five top-ranking species most commonly identified in interviews as crop raiders (accounting for >99% of summed weighted scores) were designated as crop raiders. The mean adult body mass of crop raider and non-raider species was summed per camera. Because camera traps may fail to detect some group members, we simply defined detections as a single adult of undetermined sex. Species-specific camera-trap detections were then multiplied by the species body mass (data from Carboneras, 1992; Dunning, 1992; Baptista *et al.*, 1997; Emmons and Feer, 1997; Nowak, 1999; and CA Peres (unpubl. data), Appendix A).

We estimated a primary forest habitat selectivity index for each vertebrate species by summing the total number of detections per species and associated CTNs for all deployments either within or outside of primary forest. Camera trap rates (CTR) per habitat type was therefore estimated as the number of independent detections per species divided by the total sampling effort (CTN). The habitat selectivity index for any given species *i* is then defined as a log-abundance ratio that handles zero detections as: $\log_{10} [((\text{detections}_{\text{non-primary forest (i)}} + 0.1) / \text{functioning camera trap days}_{\text{non-primary forest (i)}}) / ((\text{detections}_{\text{primary forest (i)}} + 0.1) / \text{functioning camera trap days}_{\text{primary forest (i)}})]$, whereby values smaller than 0 represent greater primary forest habitat specificity.

3.2.3 Local Interviews

Interviews were conducted in Portuguese by the authors and without the aid of translators. Interviews were recorded using a structured questionnaire and a Dictaphone, and cross-checked for accuracy. Interviewees were reassured that data would be kept anonymous and confidential (see interview script, Appendix B). Interviewees were not paid, but some were participating in paid work such as camera trapping at the time of interviews.

A total of 157 interviews were conducted at 47 local communities or city neighbourhoods (hereafter, *communities*). Interview topics included household-scale livelihoods, diet, hunting, farming, human wildlife conflict, and crop raiding (See interview script and data processing, Appendices B and C2). In 107 interviews representing 24 communities, HMC asked respondents about the *roçados* they were currently cultivating or collecting (N = 238). *Roçado*-specific questions included distance from the community, surrounding habitat, number of manioc stems (a) planted (by manioc type), (b) lost to early floods, in the case of floodplain *roçados*, (c) lost to crop raiders and (d) successfully harvested. Several *roçado* interviews were conducted per community, but respondents were chosen from different extended households to ensure their *roçados* were independent from one another.

3.2.3 Data analysis

Spatial variables were extracted in ArcGIS (10.3), and all statistical analyses were conducted in R (2.15.1). Collinearity between independent variables was tested for using Spearman’s Rank and Kruskal-Wallis Rank Sum tests. Where explanatory variables had bivariate Rho >0.70 or p <0.05, they were modelled separately.

For each camera-trap deployment, the area of deforestation and *várzea* forest within a 500m buffer was calculated using data from INPE PRODES, 2009, Hansen *et al. (*2013) Global Forest Change and RADAMBRASIL vegetation polygons (Veloso 1982; Appendices C3 and C4). Per *roçado*, the amount of adjacent habitat disturbance and extent of *várzea* was also determined through interview scores (Appendix C5).

The number of households within 4 km (Manhattan distance) of each deployment were summed. We used spatially explicit household data from the IBGE (Brazilian Institute for Geography and Statistics) 2009 Population Census of rural households, which were validated against IBGE 2007 census data (Appendix C6). A transport network accounting for all main rivers, tributaries, known navigable perennial streams, roads and known tracks in the vicinity of all surveyed communities and camera deployments was constructed from GPS track-logs taken over successive fieldwork years. We used the Network Analyst to calculate the Manhattan or “transport” distance between deployments and households across the entire study region. Per *roçado*, the number of households in the nearest community was recorded (Appendix C7). The Manhattan distance from the nearest community was calculated using the transport time and mode of transport reported from interviews, and average transport velocity (Parry and Peres, 2015, Appendix C8). Per deployment and surveyed community, the population of and distance to the nearest town was calculated using the aforementioned transport network and the IBGE (2007) census data.

Spearman’s rank correlation tests were performed to ascertain the degree to which (a) species reported to enter *roçados* were detected by cameras outside primary forest, and (b) species reported to crop raid were reportedly hunted. When comparing camera trap and interview data, primates were excluded as these were not reliably detected by cameras and interview scores for all small-bodied armadillos (order *Cingulata*) were summed because these were not differentiated in camera trap data.

Generalised Linear Mixed Effects Models (GLMMs) were created using the *glmmadmb* function to explain (1) the number of manioc stems lost to crop raiders, (2) crop raider biomass, and (3) non-crop-raider biomass. The total number of manioc stems planted that had not been lost to flooding and the number of months since the *roçado* was brought into cultivation were used as offset variables for the former models. The number of functioning camera trap nights was used as the offset variable for latter models. Offset variables were log transformed, and the surveyed community was designated as a random effect.

Habitat disturbance (interview score or deforestation within 500m), *várzea* (interview score or *várzea* within 500m), local human population density (number of mapped households within a 4-km travel buffer, centred around each camera trap station), distance from community to *roçado* (Raided models only), distance to nearest city, population of nearest city, and habitat type in which camera-traps were deployed in (Biomass models only) were designated as explanatory variables. Continuous explanatory variables were scaled to aid model convergence and comparisons of effect size.

In 40% of the *roçados,* no manioc plants were reported as lost to raiders. Semi-subsistence agriculturalists are acutely aware of agricultural losses, are adept observers at detecting animal signs, and are unlikely to fail to detect them. Therefore, we do not consider the data to be zero-inflated. To model losses to crop raiders we chose both GLMMs and Generalised Linear Mixed Effect Hurdle Models (GLMMHs) that separately explore whether a *roçado* is raided and how many stems were lost. In all cases a Poisson error structure resulted in overdispersion. In GLMMH zero models, a Binomial error structure was used. In GLMMH count models, truncated Negative Binomial structure failed to converge, therefore truncated QuasiPoisson was used. GLMMs were used for Biomass models because the biomass data included far fewer zeros. A Negative Binomial error structure was Preferred over QuasiPoisson because it deals explicitly with dispersion and AIC values are produced which can be used to aid model selection.

Models were selected using supervised backwards stepwise deletion. Explanatory variables with the highest p-value was sequentially removed, unless this resulted in an increase in ΔAIC > 2, until a minimum adequate model was reached. Variables were then sequentially deleted and ΔAIC was used to determine if additional deletions were warranted. If no variable was retained, variables with the lowest p value were sequentially added back into the model and compared to the null model to achieve the lowest AIC. Extraneous categorical variables including (1) camera model, (2) recorded media (photos vs video), (3) identity of camera deployer, and (4) deployment season, were collinear and therefore not included altogether, but added individually into the best performing Biomass models to check for significance and ΔAIC. As none of these variables were found to be significant or to lower AIC values, they were excluded from further analyses.

Species composition was analysed using Nonmetric Multidimensional Scaling (NMDS) and permutational Anova (permanova) analyses (Anderson, 2001). Detections per species per deployment were divided by CTN per deployment and multiplied by 100 to derive the standardised detection rate per 100 CTNs. Data were sqrt-transformed to reduce the influence of very common species (Clarke and Warwick, 2001). The metaMDS function (using 2 dimensions, Bray Curtis distance, and 100 random starts) was used to perform NMDS. Resultant stress, non-metric and linear fit were evaluated using a stress plot. Increasing dimensions lowered the stress, but we chose to use two dimensions for greater ease of graphical presentation and interpretation.

Permanova analysis was performed using the Bray Curtis distance between deployments using the “Adonis” function and explanatory variables from the Biomass models. Explanatory variables were tested individually, because our sampling was unbalanced between factors.

3.3 Results

3.3.1 Crops

Our 107 interviews targeted to 238 *roçados* represent a total of 1,961,575 manioc stems planted. Assuming the mean stem density (1.1 plants per m²), which was largely constant across communities, a mean yield of 6.5 sacks of farinha per 1000 stems, and an average of US$12.41 per sack of farinha (as reported by interviewees; inflation-uncorrected 2015 transaction prices), this corresponds to an aggregate *roçado* area of 1,783,250 m², a potential yield of 12,750.2 sacks of farinha, which would have been worth some US$158,230.5 Of this total, 2.2% was lost to an early flood pulse and an additional 5.5% was lost to all crop raiders. At the 189 *roçados* for which we have data per manioc type, 64.1% and 35.9% of manioc stems planted was bitter and sweet manioc, respectively. Overall losses to crop raiders were 3.7% for bitter manioc and 9.3% for sweet manioc (Fig. 3.2).

On average, 11,009.4 (± 894.9) manioc stems were planted in one or more *roçados* each year per respondent, including 58.0 ± 3.5% of bitter manioc and 42.0 ± 3.5% of sweet manioc (Appendix C9). Of these, 2.1 ± 1.0% were lost to unexpected floods, 8.0 ± 1.2% were raided, and it was reported that 74.0 ± 3.0% stems would have been raided if crop-raiders were neither discouraged nor depleted by hunters. An estimated 4.7 ± 1.2% and 15.8 ± 2.9% of bitter and sweet manioc were lost to crop-raiders, respectively. However, those proportions would have increased to 37.1 ± 8.4% for bitter manioc and 85.7 ± 9.2% for sweet manioc in the absence of hunting.

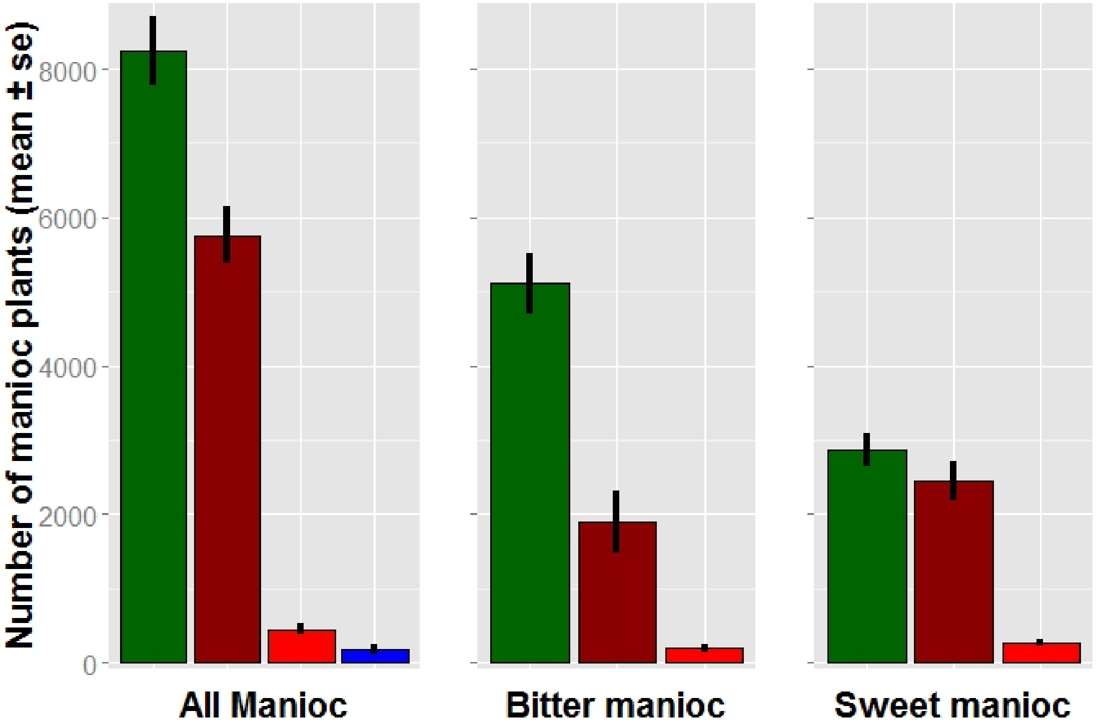


***Figure 3.2**. Summary number of manioc stems planted and lost per agricultural plot (*roçado*), separated by type of manioc, on the basis of interview data. Dark green and dark red bars respectively indicate the mean total number of manioc stems planted per roçado, and those that would have been lost if crop raiders were not suppressed by hunting. Red bars indicate the number of manioc stems actually lost to crop raiders, and blue bars indicate those lost to flooding (only available for "All Manioc"). Vertical black lines represent standard errors.*

Interviewees had resided in their respective communities for 20.1 ± 1.3 years. Mean journey time to *roçados* from the community was 30.6 ± 2.8 minutes. Lethal methods to suppress crop raiders included hunting (38.0% of all responses), using dogs (17.1%), traps (3.2%), and shooting (0.6%) (Fig. 3.3). Nonlethal methods included tending the *roçado* and maintaining vigilance (12.0%), using scarecrows (7.6%), firebreaks (7.0%), scaring animals away (4.4%), enclosing *roçados* with nets (3.2%), maintaining the *roçado* weed-free (3.2%) and praying (0.6%). Only 2.5% reported doing nothing to combat raiders, often because their *roçado* plot was too far away, and 0.6% that their *roçados* did not succumb to crop raiders, thereby requiring no response.

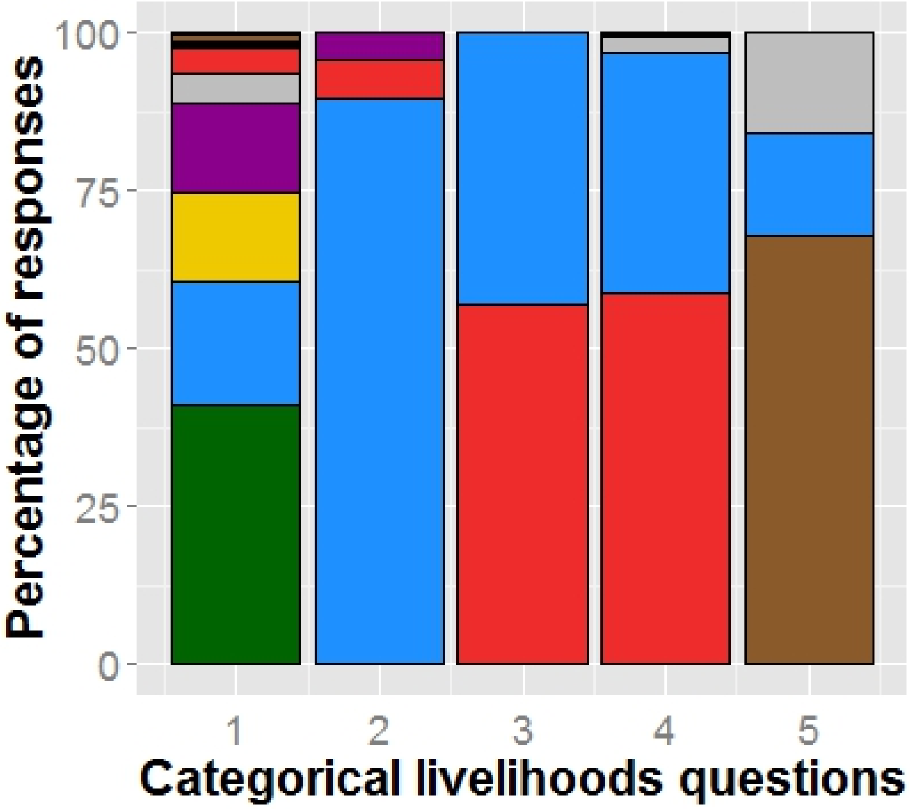


Figure 3.3. *Stacked bars summarising responses to categorical interview questions. Bar segment height represents the percentage of responses or weighted responses.* ***Bar1*** *= Ranked livelihood activities. Green = agriculture. Blue = fishing. Gold = Welfare and PES payments. Purple = extractivism. Grey = salaried work. Red = hunting. Black = other. Brown = timber. Orange (imperceptible) = livestock.* ***Bar2*** *= Ranked protein sources. Blue = caught wild fish. Red = hunted game meat. Purple = equally important.* ***Bar3*** *= "Have you killed animals in your* roçados*?" Red = "yes". Blue = "no".* ***Bar4*** *= Response to crop raiders. Red = lethal. Blue = nonlethal. Grey = nothing. Black = crop raiders do not invade.* ***Bar5*** *= method of transport to roçado. Brown = on foot. Blue = un-motorised canoe. Grey = canoe with outboard motor.*

3.3.2 Crop-raiders and other species

The prevalence of vertebrate species detected by camera traps or reported in interviews was widely variable (Fig. 3.4). In total, 27 taxa were reported to enter *roçados*, especially caviomorph rodents, cervids, tayasuids, armadillos, tapirs and felids. Ten of these species were reported to raid crops, five of which (*Dasyprocta fuliginosa, Pecari tajacu, Cuniculus paca, Mazama americana and Echimyidae spp* in order of importance) were rodents or ungulates representing >99% of weighted crop raiding scores.

A total of 33 vertebrate taxa were reliably detected by camera traps, which yielded a shallower rank-abundance curve than did interview data. The three most frequently detected species overall (*Dasyprocta fuliginosa*, *Mazama Americana* and *Cuniculus paca*) were also frequently reported crop raiders and were proportionally equally detected in either primary forest or successional mosaics. Species frequently reported to enter *roçados* were also frequently detected by cameras outside primary forest (Spearman's Rho = 0.47; Fig. 3.5).

Nineteen taxa were frequently hunted, and these were often reported as crop raiders ($p<0.001$, Spearman's Rho = 0.41). The first (*Tayassu pecari*) and seventh (*Tapirus terrestris*) most commonly reported hunted species, however, were infrequently camera-detected large-bodied ungulates that were not reported as crop raiders. Seven taxa were reportedly killed at *roçados*, the four top-ranking of which were also the four top-ranking crop raiders.

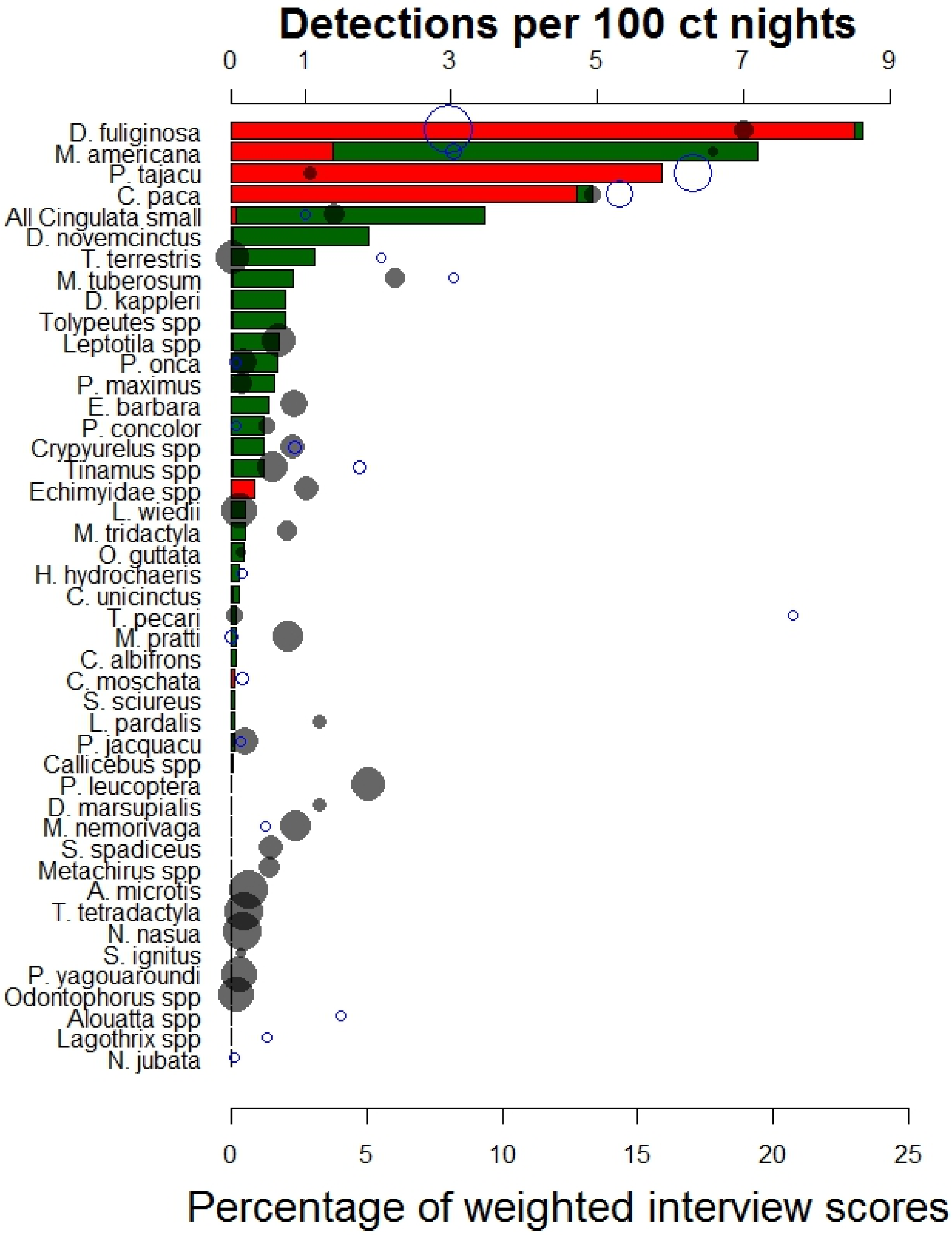


Figure 3.4: *Species prevalence in interviews and camera detections. Values in Appendix A.* ***i)*** *Stacked bar length represents species propensity to enter roçados as reported in interviews. Red = considered a crop raider. Green = not considered a crop raider* ***ii)*** *Transparent black circles - position along x axis represents standardised detection frequency per 100 CTN. Circle size represents the degree to which the species was detected in primary forest* ***iii)*** *Empty blue circles – position along x axis represents the percentage of weighted interview scores reporting the species as hunted. Circle size represents the frequency of that species being reportedly killed in roçados (larger = higher frequency).*

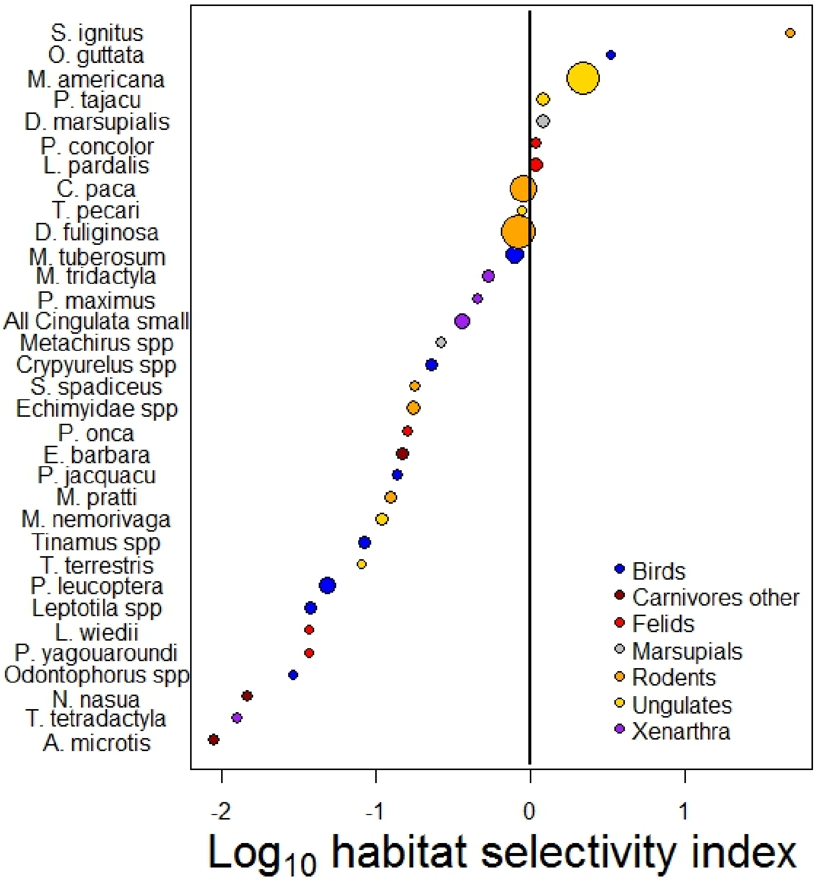


Figure 3.5: Log_{10} habitat selectivity index score and detection rate per species derived from camera trap data. Larger circles indicate higher CTR. HSI Scores < 0 indicate the species had a higher detection rate in primary forest. Colour represents taxonomic group as indicated in the legend.

3.3.3 Determinants of crop-raiding rates

Crop raider biomass detected by cameras increased with distance to the nearest town (Table 3.1). In contrast, non-raider biomass was related to habitat type, with more pristine forest habitats exhibiting higher biomass. GLMM models indicate that reported losses to crop raiders decreased in heavily-settled areas. When modelled using GLMMHs, local human population density and habitat score (a higher score representing less disturbed habitat) both negatively influenced the chance of a *roçado* being raided, whereas human density alone negatively influenced the amount lost to raiders.

Table 3.1. *. Key predictors of the magnitude of manioc crop losses, crop-raider (and non-raider) biomass, and species composition sampled by camera-traps. Each row represents a retained independent variable. For methodological details and variable derivation, see methods and Appendix C. Reference habitat is primary forest.*

Model number	**Data type**	**Dependent variable**	**Model type**	**Model family**	**Retained independent variable**	**R²**	**Odds ratio**	**Lower confidence interval**	**Upper confidence interval**	**P value**
1	Interview	Crop Losses	GLMM	Negative Binomial	Local Human Population	NA	0.50	0.30	0.83	<0.01
2	Interview	Crop Losses	Hurdle - Zero	Binomial	Local Human Population	NA	0.35	0.22	0.56	<0.001
2	Interview	Crop Losses	Hurdle - Zero	Binomial	Habitat Intactness - Score	NA	0.72	0.52	0.99	<0.05
3	Interview	Crop Losses	Hurdle - Count	Truncated QuasiPoisson	Local Human Population	NA	0.74	0.55	1.00	>0.05 (0.053)
4	Camera trap	Crop Raider Biomass	GLMM	Negative Binomial	Distance to Nearest City	NA	1.34	1.02	1.76	<0.05
5	Camera trap	Non-Raider Biomass	GLMM	Negative Binomial	Habitat - Disturbed Forest	NA	0.58	0.20	1.68	>0.05
5	Camera trap	Non-Raider Biomass	GLMM	Negative Binomial	Habitat - Capoeira	NA	0.52	0.30	0.90	<0.05
5	Camera trap	Non-Raider Biomass	GLMM	Negative Binomial	Habitat - Homestead	NA	0.20	0.09	0.42	<0.001
6	Camera trap	Species Composition	Permanova	NA	Habitat	0.07	NA	NA	NA	<0.001
7	Camera trap	Species Composition	Permanova	NA	Habitat Intactness - Deforestation	0.02	NA	NA	NA	<0.01

NMDS ordination based on a Bray-Curtis distance matrix suggests that the species composition of CT stations within successional mosaics represents a nested subset of species in primary forest (Fig. 3.6). In ordination space, less disturbed forest habitat occupies the largest area, with more disturbed habitats occupying small subsets, rather than a distinct space. Similarly, the main crop raiding species are clustered in ordination space, whilst the larger number of non-raider species are spread widely. Permanova analyses showed significant bivariate associations with habitat category and primary forest conversion. Modest R^2 values indicate that the variables tested did not explained much of the variation. The variable with the highest R^2 and lowest p value was habitat category.

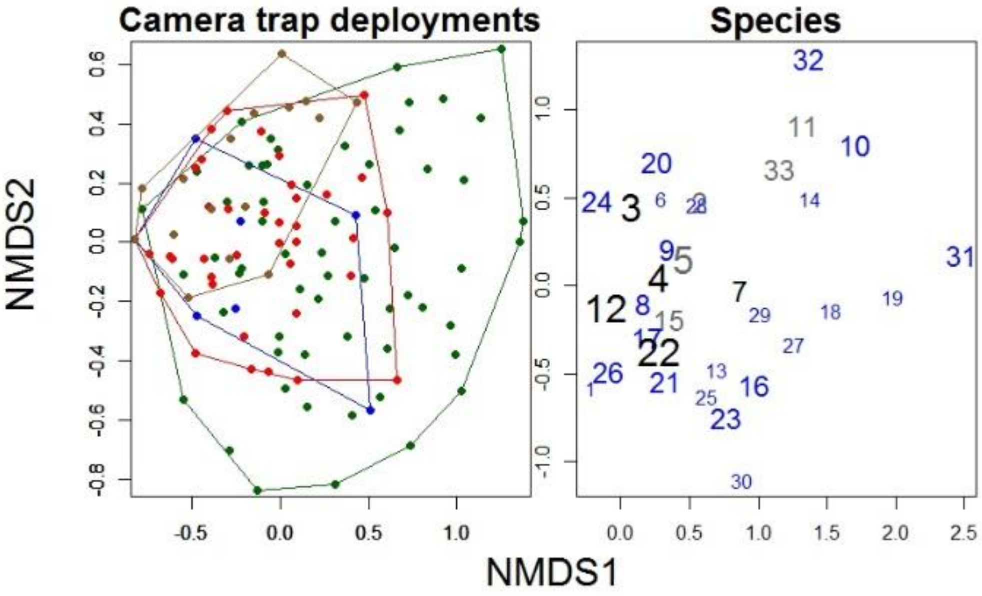


Figure 3.6**. Ordination plots representing Bray Curtis distances from a matrix of standardised camera trap data.* ***Left panel *– Circles and convex hulls represent habitat categories, where dark green, blue, red and brown represent primary forest, disturbed forest, secondary forest and homestead, respectively.* ***Right panel*** *– Number size and colour represent species propensity to enter roçados and to crop raid, whereby larger number indicate a higher propensity to enter roçados, black, grey and blue represent frequent crop raiders, infrequent crop raiders and non-raiders, respectively. Species are numbered as followed. 1* = A. microtis, *2* = Crypturellus. Spp, *3* = C. paca, *4* = D. fuliginosa, *5* = Dasypus. Spp, *6* = D. marsupialis, *7* = Echimyidae. Spp, *8* = E. barbara, *9* = L. pardalis, *10* = L. wiedii, *11* = Leptotilla. Spp, *12* = M. americana, *13* = M. nemorivaga, *14* = Metachirus. Spp, *15* = M. tuberosum, *16* = M. pratii, *17* = M. tridactyla, *18* = N. nasua, *19* = Odontophorus. Spp, *20* = O. guttata, *21* = P. onca, *22* = P. tajacu, *23* = P. jacquacu, *24* = P. maximus, *25* = P. leucoptera, *26* = P. concolor, *27* = P. yagouaroundi, *28* = S. iginitus, *29* = S. spadiceus, *30* = T. tetradactyla, *31* = T. terrestris, *32* = T. pecari, *33* = Tinamus. Spp.

3.4 Discussion

3.4.1 The significance of losses to terrestrial vertebrate crop raiders

Terrestrial vertebrate crop raiding imposes a triple burden for semi-subsistence forest dwellers in Amazonia. Firstly, although apparently modest, the overall mean reported losses to raiders of 5.5% are substantial, and mask large variability to the extent that some farmers every year are ruined (c.f. Naughton-Treves, 1998). Losses to crop raiders compound the hardship faced by semi-subsistence farmers, whose livelihoods are additionally impacted by flooding. Secondly, though sweet manioc is more palatable and requires less arduous processing (Frazer, 2010), the nearly triple raiding rates associated with it, seemingly relegate it to a secondary horticulture within *roçados*. Lastly and perhaps most importantly (Barua *et al*., 2013), farmers invest substantial effort in protecting their fields, incurring attendant opportunity costs, and would suffer nearly tenfold crop losses if they did not. The effects of guarding range from precluding extremely high losses (Gillingham and Lee, 2003; Pérez and Pacheco, 2006) to largely ineffective (Linkie *et al*., 2007). All anti-raider tactics along the Juruá, including setting nets, traps, hunting with dogs, and creating scarecrows and firebreaks are labour-intensive, which is consistent with other studies. For example Ugandan famers spend over 20% of their time guarding against crop raiders in some months (Hill 2000), and Tanzanian farmers guard their fields on a full time basis during high-risk months (Gillingham and Lee 2003).

More isolated farmers living in small communities far from towns experienced the highest losses to crop raiders. This has been reported in other crop raiding studies (Hill, 2000; Naughton-Treves *et al.,* 2003). These remote, low-density communities have the highest barriers to market and lowest incomes (Parry *et al.,* 2010), thereby suggesting a triple disadvantage in terms of their socioeconomic welfare. Several urban respondents reported that past losses to crop raiders were much higher. A respondent from a Carauari suburb reported that he “used to see cutias (*Dasyprocta fuliginosa*) eating manioc five times in one day. Now there are not even tracks.” This may reflect expanding urban populations with attendant increases in hunting pressure and disturbance.

3.4.2 Hunting crop raiders

Potentially, hunting crop raiders around *roçados* is a ‘win-win’ strategy, reducing rates of raiding and providing meat for local communities (Smith, 2005). Furthermore, as terrestrial vertebrate crop raiders are often fecund, disturbance tolerant, and ubiquitous species, they are good candidates for sustainable subsistence hunting.

Despite this, and in agreement with Naughton-Treves *et al.,* (2003), who found that on average, crop losses to raiders were more valuable than hunting gains in terms of meat acquisition, we found that hunting crop raiders may provide limited benefit to semi-subsistence agriculturalists in our study area insofar as (1) nonlethal methods to suppress crop raiders were almost as commonly reported as lethal methods; (2) Terrestrial game hunting in the Medio Juruá is secondary to fish as a source of animal protein (Endo et al. 2016), and a modest livelihood component (Newton et al., 2012), which is consistent with other studies of *ribeirinho* communities in lowland Amazonia (Murrieta *et al.,* 1999; Adams *et al., 2009*) and (3) the most hunted species, white-lipped peccary (*Tayassu pecari*), is not considered a significant crop raider as its large herds rarely entered *roçado* areas.

Notwithstanding this, Naughton-Treves *et al.*, (2003) encouragingly found that in remote areas where hunting pressure has not greatly reduced large game abundance, hunting gains compensate crop losses. This supports the notion that community location represents a livelihood trade-off between access to natural resources and access to goods and services (Parry *et al.*, 2010*).*

We also found that the most prolific crop raiding species were amongst the most commonly hunted. The nineteen species reportedly hunted in our study accord with game offtake profiles reported in other Neotropical studies (Redford and Robinson, 1987; Jerozolimski and Peres, 2003). Likewise, the species identified in our study as the most burdensome crop raiders were also identified by Pérez and Pacheco (2006) and Naughton-Treves et al., (2003). *Tayassu pecari* is anomalous. Foraging in large herds and ranging over large areas (Peres, 1996; Fragoso, 1998), this species is a stochastic boon for hunters and impossible to ignore even by those otherwise disinclined to hunt. Although not regarded an important crop raider due to its infrequent occurrence, several respondents commented that in the unfortunate event that a herd of *Tayassu pecari* entered their *roçado*, the entire crop would be ruined.

Additionally, the nutritional benefit of meat may be disproportionate to the quantity consumed. Indigenous Amazonian and to a lesser extent *ribeirinho* groups place extremely high nutritional and cultural importance on game meat (Neel *et al.,* 1964; Carneiro, 1970*;* Redford and Robinson, 1987*).*

Lastly, the key terms “hunting” and “livelihood”, were understood differently by respondents, some of whom did not equate carrying a gun to their *roçado* and opportunistically killing animals as hunting. They only considered hunting to be specifically setting out with the primary objective of killing game. Similarly, some respondents did not consider strictly subsistence activities such as hunting, even if those were frequently engaged in, to be a primary livelihood component. Thus our interviews may underestimate the incidence and importance of opportunistic and subsistence hunting.

3.4.3 Crop raiding species and the human landscape

Vertebrate species either reported to enter *roçados* or camera-trapped in their vicinities are a small proportion of the assemblage detected by camera traps, and crop raiders are a smaller proportion still. There are ecological, behavioural and demographic filters species must pass through if they are to become burdensome raiders. The vast majority of Amazonian forest vertebrates persist at low densities and are intolerant of highly disturbed habitats. Amongst the most habitat-generalist, disturbance-tolerant species, only a small proportion are capable of digging and ingesting manioc tubers or grazing their leaves, both of which are highly toxic to generalist herbivores (Gleadow and Woodrow, 2002). This largely explains the much higher crop-raiding rates observed for the more palatable sweet manic, which has a lower cyanide content.

The zero hurdle model retained the habitat intactness score, implying that *roçados* surrounded by more intact habitat were less likely to be raided. We anticipated the opposite effect, as neighbouring undisturbed habitat acts as a reservoir for crop raiders. Other studies have shown that crop raiding is strongly associated with areas near forest (Naughton-Treves, 1998; Hill, 2000; Linkie, 2007). This is an unexpected result that we treat with caution. Odds ratio confidence intervals suggest that the relationship is weak. It may be that Neotropical crop raiders persist in highly heterogeneous agricultural mosaics to a greater degree than anticipated. This is not the case for non-raiders, whose biomass was markedly depressed in more disturbed habitats. A more plausible explanation is the effect of landscape context. Unlike other crop-raiding study areas throughout the tropics, the Medio Juruá region largely consists of vast tracts of contiguous primary forest with deforestation and regrowth representing only ~1.8% of total area. At a landscape scale, primary forest is thus not a limited habitat and habitat-generalist raiders may be attracted to anthropogenic resources.

Though anthropogenic factors such as community size and proximity to urban centers had a negative effect on crop raiding, household distance to *roçado* did not. This is counterintuitive as *roçados* farther removed from the centre of the community are expected to experience less hunting pressure and vigilance. Whilst we can conclude that anthropogenic pressure in general influences crop raiders, we cannot confirm that this effect is spatially concentrated.

3.4.4 A forest ecosystem disservice?

Crop raiding can be considered an ecosystem disservice. Anthropogenic pressures negatively influence rates of crop raiding, so that Amazonian communities sometimes pay a high price for living at low densities in a high species-richness, intact environment. The biodiverse ecosystem per se may not be at fault. Crop raiding species tolerate human disturbance, and even much simplified ecosystems include them. Indeed, biotic disturbance and simplification may exacerbate levels of crop raiding and pests (Andow, 1983; Yamada and Muroyama, 2010). Furthermore, camera trap and interview data suggest that crop raiders are closely attended by their natural predators in faunally-intact vertebrate assemblages such as those along the Juruá, presumably buffering raiding rates. However, this is inadequate consolation to local villagers who may also incur significant losses to forest carnivores. Predators of large forest rodents *(dasyproctids and echimyids*), such as ocelots and tayras, are frequently implicated in livestock depredation. Large predators of ungulates (e.g. *Mazama americana* and *Pecari tajacu*) such as large felids (*Panthera onca* and *Puma concolor*), are feared killers of domestic pigs and cattle and occasionally people (Conforti, and de Azevedo, 2003; Soto-Shoender, and Giuliano, 2011).

3.4.5 Dog hunting

Amongst the strategies to reduce crop raiding, 17.1% of responses reported hunting with dogs, or using dogs to scare away raiders. This is a contentious issue. Dogs are believed to drastically impact local fauna (Galetti and Sazima, 2006), covering long distances, killing small game, maiming and chasing away larger animals and causing additional disturbance through their noise and scent. There have been calls to enforce bans on the use of dogs as a hunting tool in Brazil (Cunha and De Almeida, 2000; Carvalho and Pezzuti, 2010). Their common use suggests that as a tool for reducing rates of crop raiding, however, dogs have merit. One interviewee reported that their community suffered high consistent losses to collared peccary herds, until they employed a professional hunter with dogs from a nearby community to kill and scare them away. The intervention was so effective that they later acquired hunting dogs of their own.

3.4.6 Interview reliability

Our interview data likely suffers from social desirability bias (John *et al*., 2010). Our interviews included potentially sensitive topics such as livelihoods and hunting. Techniques to increase the reliability of responses to sensitive questions (randomised response techniques (RRT) or similar) were not used. Interviews were carried out by non-locals, who may be perceived as outsiders. We asked respondents to remember and quantify losses to crop raiders and to estimate counterfactual losses in the absence of crop protection. Plausibly, respondents may have been motivated to over-report losses and under-report hunting. This is because hunting may be perceived to be an activity that researchers disapprove of, whilst high crop losses not only highlight livelihood challenges, but justify hunting.

Nonetheless, we argue that our data are trustworthy. Our research group has been active in the Medio Jurua region since 2007 and has built trust through involvement in popular and successful resource management programs such as pirarucu (*Arapaima spp*) fisheries. Interviewers built trust by acting respectfully towards local communities (see Appendix C.10). We asked potentially sensitive questions in a direct manner, trusting the respondents rather than employing RRT.

The consistency of our interview results both with comparable existing studies (Naughton-Treves, 1998; Hill, 2000; Nchanji 2002) and with our camera data, increases our confidence in them. A coherent picture emerges due to the complementarity between camera trap and interview data, suggesting that the data are broadly reliable. Species frequently detected by cameras, especially in disturbed habitats, were those reported to frequent *roçados*. Likewise, nearby human population density (as quantified by community size or proximity to city), was associated with both lower reported crop losses and with lower detected crop raider biomass. By contrast habitat disturbance (measured by habitat type or amount of nearby deforestation), was associated with lower non-raider biomass and simplified species composition. Given the complementary strengths and weaknesses of these two data collection methods, we suggest that mixed methods hold promise for understanding socio-ecological problems.

3.5 Conclusions

Terrestrial vertebrate crop raiding represents a burdensome ecosystem disservice for rural Amazonians, who invest substantial amounts of time energy in protecting crops to avoid significant losses. Crop raiding is heightened in sparsely settled areas, thereby compounding the economic hardship faced by small communities that are already disadvantaged by isolation from the material, service and information economy of urban centres. Crop raiders comprise a select group of habitat-generalist, disturbance-tolerant and relatively fecund species, which apparently make them ideal candidates for sustainable subsistence hunting. However, local semi-subsistence communities consider high crop raider biomass to be a livelihood threat, rather than a hunting opportunity.

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APPENDIX A

Table B1

Summarised camera trap, interview and trait data per species. Camera trap data do not distinguish between small armadillos. NA indicates species not reliably detected by camera traps or habitat selectivity index cannot be calculated because camera detections are zero. CTR = Detections per 100CT Nights (all habitats). HSI = Habitat Selectivity Index. Interview data are percentages of summed weighted scores. Body Mass sources a = Baptista et al.*, 1997, b = Dunning, 1992, c = Emmons and Feer, 1997, d = Carboneras, 1992, e = Nowak, 1999, f = Peres (unpublished). Where male and female adult biomass for a given species differ, the mean was used. Where only a range of adult biomass was known for a given species, the mean of the upper and lower limits was used.*

Binomial /Designation	Taxa	English Name	CTR	HSI	Hunted	Killed in *Roçados*	Enters *Roçados*: Crop Raider	Enters *Roçados*: Non-Raider	Body Mass, g	Source
All Cingulata small	Xenarthra	Small Armadillos All	1.4	-0.44	2.73	0	0.14	9.17	4800	c
Alouatta spp	Primates	Howler Monkey	NA	NA	4.03	0	0	0	6500	f
Atelocynus microtis	Carnivores Other	Short-Eared Dog	0.24	-2.05	0	0	0	0	7750	c
Cabassous unicinctus	Xenarthra	Southern Naked Tailed Armadillo	NA	NA	0	0	0.04	0.23	3200	c
Cairina moschata	Birds	Muscovy Duck	0	NA	0.37	1	0.1	0	2550	d
Callicebus spp	Primates	Titi Monkey	NA	NA	0	0	0	0.07	1125	f
Cebus albifrons	Primates	White Fronted Capuchin Monkey	NA	NA	0	0	0	0.14	2700	f
Crypturellus spp	Birds	Tinamou Small	0.83	-0.64	2.35	1	0.07	1.1	420	f
Cuniculus paca	Rodents	Paca	4.92	-0.04	14.36	12	12.74	0.58	9500	f
Dasyprocta fuliginosa	Rodents	Agouti	6.99	-0.07	8.01	53	23.02	0.29	4500	f
Dasypus kappleri	Xenarthra	Greater Long-Nosed Armadillo	NA	NA	0	0	0.04	1.96	10150	c

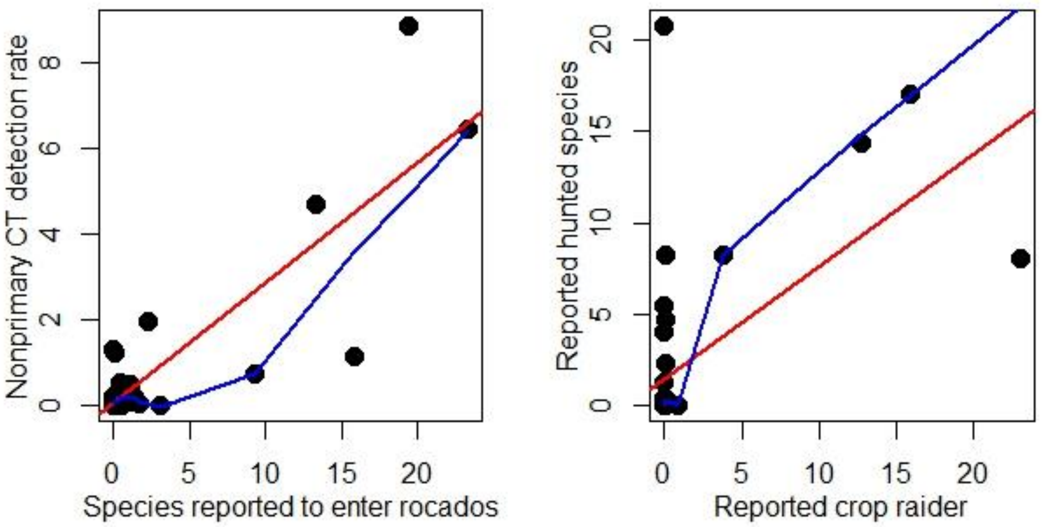
Binomial /Designation	Taxa	English Name	CTR	HSI	Hunted	Killed in *Roçados*	Enters *Roçados*: Crop Raider	Enters *Roçados*: Non-Raider	Body Mass, g	Source
Didelphis marsupialis	Marsupials	Common Opossum	1.19	0.09	0	0	0	0	1088	c
Echimyidae spp	Rodents	Spiny Rat	1.02	-0.75	0	0	0.84	0	560	c
Eira barbara	Carnivores Other	Tayra	0.86	-0.83	0	0	0	1.35	4850	c
Hydrochoerus hydrochaeris	Rodents	Capybara	0	NA	0.41	0	0	0.29	50000	c
Lagothrix spp	Primates	Woolly Monkey	NA	NA	1.31	0	0	0	8710	f
Leopardus pardalis	Felids	Ocelot	1.21	0.04	0	0	0	0.09	15000	f
Leopardus wiedii	Felids	Margay	0.1	-1.43	0	0	0	0.52	6000	c
Leptotila spp	Birds	White Tipped Dove	0.64	-1.42	0	0	0.07	1.67	149	a
Mazama americana	Ungulates	Red Brocket Deer	6.57	0.34	8.22	6	3.77	15.63	30000	f
Mazama nemorivaga	Ungulates	Grey Brocket Deer	0.89	-0.96	1.25	0	0	0	18000	f
Metachirus spp	Marsupials	Brown Four-Eyed Opossum	0.52	-0.57	0	0	0	0	390	c
Mitu tuberosum	Birds	Razor-Billed Curassow	2.23	-0.1	8.21	0	0.07	2.22	3000	f
Myoprocta pratti	Rodents	Green Acouchi	0.78	-0.9	0	1	0	0.14	750	f
Myrmecophaga tridactyla	Xenarthra	Giant Anteater	0.76	-0.27	0	0	0	0.48	30500	c
Nasua nasua	Carnivores Other	Coati	0.14	-1.83	0	0	0	0	5100	c
Neochen jubata	Birds	Orinoco Goose	0	NA	0.13	0	0	0	1396	d
Odontophorus spp	Birds	Wood Quail	0.07	-1.54	0	0	0	0	310	f

Binomial /Designation	Taxa	English Name	CTR	HSI	Hunted	Killed in *Roçados*	Enters *Roçados*: Crop Raider	Enters *Roçados*: Non-Raider	Body Mass, g	Source
Panthera onca	Felids	Jaguar	0.17	-0.79	0.15	0	0	1.7	80000	f
Pecari tajacu	Ungulates	Collared Peccary	1.07	0.09	17	25	15.89	0	25000	f
Penelope jacquacu	Birds	Spix's Guan	0.19	-0.86	0.32	0	0	0.08	1280	f
Priodontes maximus	Xenarthra	Giant Armadillo	0.14	-0.34	0	0	0	1.59	30000	c
Psophia leucoptera	Birds	Pale Winged Trumpeter	1.88	-1.31	0	0	0	0	1200	f
Puma concolor	Felids	Puma	0.48	0.04	0.15	0	0	1.17	45000	c
Puma yagouaroundi	Felids	Jaguarundi	0.1	-1.43	0	0	0	0	8000	f
Saimiri sciureus	Primates	Squirrel Monkey	NA	NA	0	0	0	0.1	940	f
Sciurus ignitus	Rodents	Bolivian Squirrel	0.12	1.68	0	0	0	0	700	f
Sciurus spadiceus	Rodents	Southern Amazon Red Squirrel	0.54	-0.74	0	0	0	0	1200	f
Tamandua tetradactyla	Xenarthra	Southern Tamandua	0.17	-1.9	0	0	0	0	4500	c
Tapirus terrestris	Ungulates	Tapir	0.02	-1.09	5.5	0	0	3.09	160000	f
Tayassu pecari	Ungulates	White Lipped Peccary	0.05	-0.05	20.74	0	0	0.19	32000	f
Tinamus spp	Birds	Tinamou Large	0.57	-1.07	4.75	1	0.07	1.1	1200	f
Tolypeutes spp	Xenarthra	Three Banded Armadillo	NA	NA	0	0	0.04	1.96	1300	e

Table B2

Summary Camera Trap Data

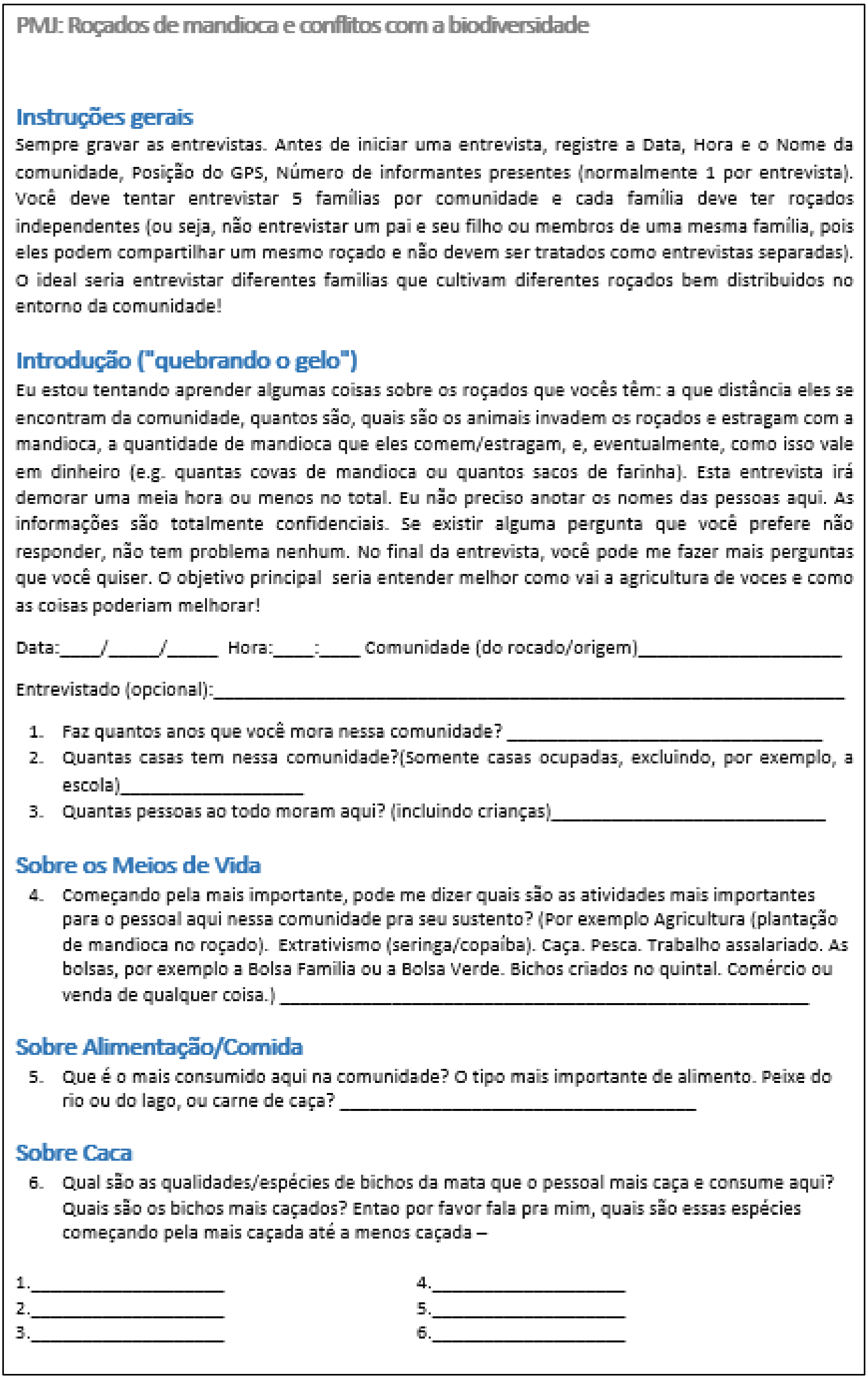
Metric	Units	Mean	N	Standard Deviation	Standard Error	Sum Total
Camera Deployment Duration	Camera trap nights	31.87	132	5.64	0.49	4206.21
Distance to Nearest Camera	m	974.40	132	1997.86	173.89	NA
Biomass of Crop Raiders Detected	kg	96.47	132	128.38	11.17	12734.05
Biomass of Non-Raiders Detected	kg	41.54	132	51.27	4.46	5483.80
Wild Species Richness	N species	4.80	132	3.40	0.30	32.00
N Detections		11.75	132	11.95	1.04	1551.00
Diversity	Shannon Index Reciprocal	3.27	132	2.08	0.18	NA
Várzea Within 500m of camera	m^2	232132.89	132	284243.71	24740.24	NA
Deforestation Within 500m of camera	m^2	218736.14	132	185650.32	16158.79	NA
Households Within 4km (travel distance) of camera	N households	16.77	132	16.70	1.45	NA
Fluvial Distance to Nearest City	m	132161.75	132	61403.25	5344.47	NA
Population of Nearest City	N households	3310.45	132	1422.25	123.79	NA



Supplementary Figure 3.1. *Scatter plots of interview and camera data per species. Linear regression lines (red) and lowess lines (blue). Left – The relationship between a species propensity to enter roçados as reported in interviews, and the camera trap rate outside of primary forest.* $p<0.001$, *adjusted* $R^2= 0.73$. *Spearman's Rho = 0.47. Right – The relationship between a species propensity to crop raid as reported in interviews, and its importance as a hunted species as reported in interviews.* $p<0.001$, *adjusted* $R^2 = 0.32$. *Spearman's Rho = 0.41.*

APPENDIX B

Interview Script



PMJ: Roçados de mandioca e conflitos com a biodiversidade

Instruções gerais

Sempre gravar as entrevistas. Antes de iniciar uma entrevista, registre a Data, Hora e o Nome da comunidade, Posição do GPS, Número de informantes presentes (normalmente 1 por entrevista). Você deve tentar entrevistar 5 famílias por comunidade e cada família deve ter roçados independentes (ou seja, não entrevistar um pai e seu filho ou membros de uma mesma família, pois eles podem compartilhar um mesmo roçado e não devem ser tratados como entrevistas separadas). O ideal seria entrevistar diferentes familias que cultivam diferentes roçados bem distribuidos no entorno da comunidade!

Introdução ("quebrando o gelo")

Eu estou tentando aprender algumas coisas sobre os roçados que vocês têm: a que distância eles se encontram da comunidade, quantos são, quais são os animais invadem os roçados e estragam com a mandioca, a quantidade de mandioca que eles comem/estragam, e, eventualmente, como isso vale em dinheiro (e.g. quantas covas de mandioca ou quantos sacos de farinha). Esta entrevista irá demorar uma meia hora ou menos no total. Eu não preciso anotar os nomes das pessoas aqui. As informações são totalmente confidenciais. Se existir alguma pergunta que você prefere não responder, não tem problema nenhum. No final da entrevista, você pode me fazer mais perguntas que você quiser. O objetivo principal seria entender melhor como vai a agricultura de voces e como as coisas poderiam melhorar!

Data:____/_____/_____ Hora:____:____ Comunidade (do rocado/origem)______________________

Entrevistado (opcional):____

1. Faz quantos anos que você mora nessa comunidade? ___________________________________
2. Quantas casas tem nessa comunidade?(Somente casas ocupadas, excluindo, por exemplo, a escola)____________________
3. Quantas pessoas ao todo moram aqui? (incluindo crianças)______________________________

Sobre os Meios de Vida

4. Começando pela mais importante, pode me dizer quais são as atividades mais importantes para o pessoal aqui nessa comunidade pra seu sustento? (Por exemplo Agricultura (plantação de mandioca no roçado). Extrativismo (seringa/copaiba). Caça. Pesca. Trabalho assalariado. As bolsas, por exemplo a Bolsa Familia ou a Bolsa Verde. Bichos criados no quintal. Comércio ou venda de qualquer coisa.) ____

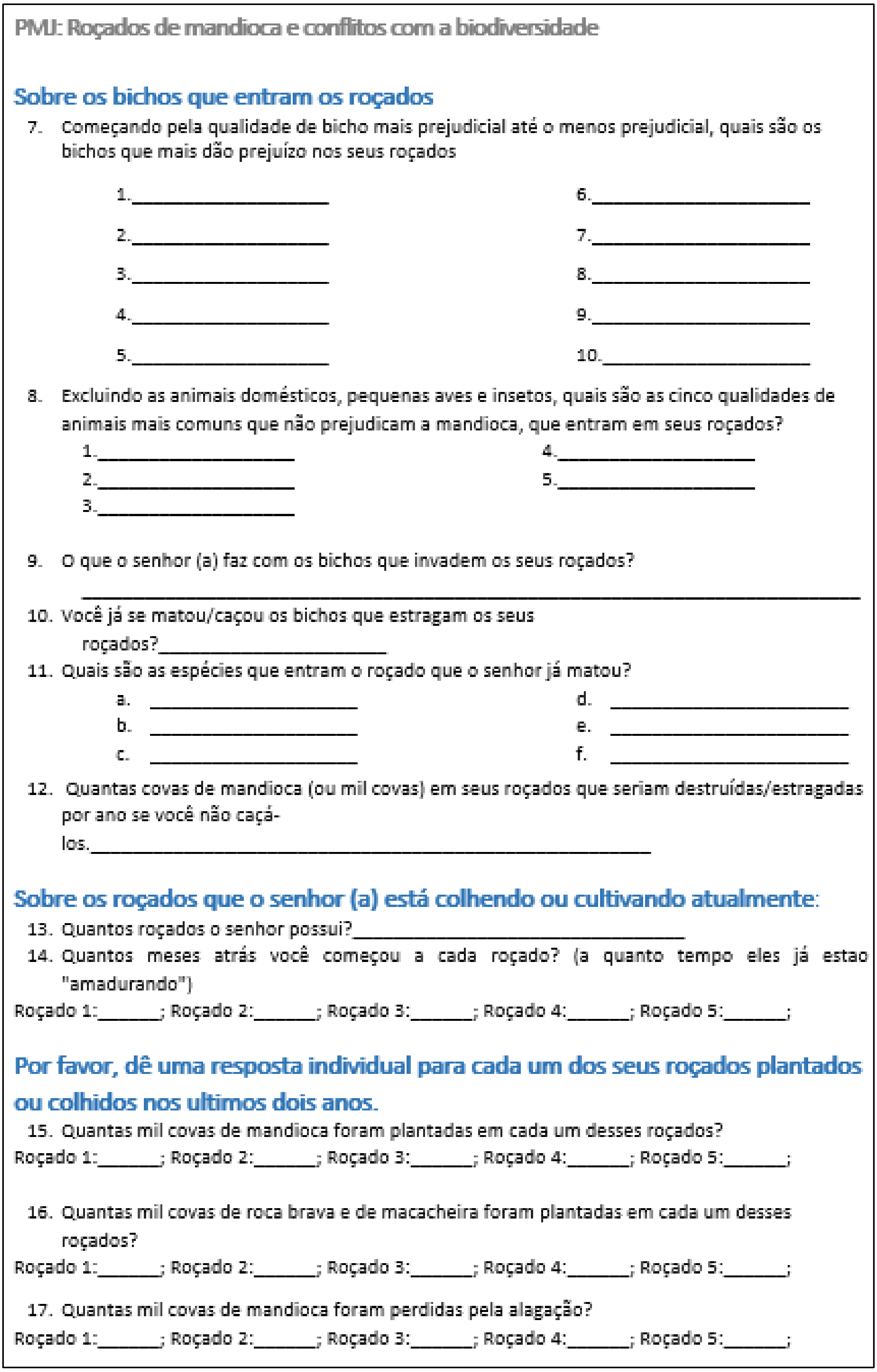
Sobre Alimentação/Comida

5. Que é o mais consumido aqui na comunidade? O tipo mais importante de alimento. Peixe do rio ou do lago, ou carne de caça? _______________________________________

Sobre Caca

6. Qual são as qualidades/espécies de bichos da mata que o pessoal mais caça e consume aqui? Quais são os bichos mais caçados? Entao por favor fala pra mim, quais são essas espécies começando pela mais caçada até a menos caçada –

1.______________________
2.______________________
3.______________________
4.______________________
5.______________________
6.______________________



PMU: Roçados de mandioca e conflitos com a biodiversidade

Sobre os bichos que entram os roçados

7. Começando pela qualidade de bicho mais prejudicial até o menos prejudicial, quais são os bichos que mais dão prejuízo nos seus roçados

1.____________________ 6.____________________
2.____________________ 7.____________________
3.____________________ 8.____________________
4.____________________ 9.____________________
5.____________________ 10.____________________

8. Excluindo as animais domésticos, pequenas aves e insetos, quais são as cinco qualidades de animais mais comuns que não prejudicam a mandioca, que entram em seus roçados?
1.____________________ 4.____________________
2.____________________ 5.____________________
3.____________________

9. O que o senhor (a) faz com os bichos que invadem os seus roçados?
____
10. Você já se matou/caçou os bichos que estragam os seus roçados?____________________
11. Quais são as espécies que entram o roçado que o senhor já matou?
a. ____________________ d. ____________________
b. ____________________ e. ____________________
c. ____________________ f. ____________________
12. Quantas covas de mandioca (ou mil covas) em seus roçados que seriam destruídas/estragadas por ano se você não caçá-los.____

Sobre os roçados que o senhor (a) está colhendo ou cultivando atualmente:

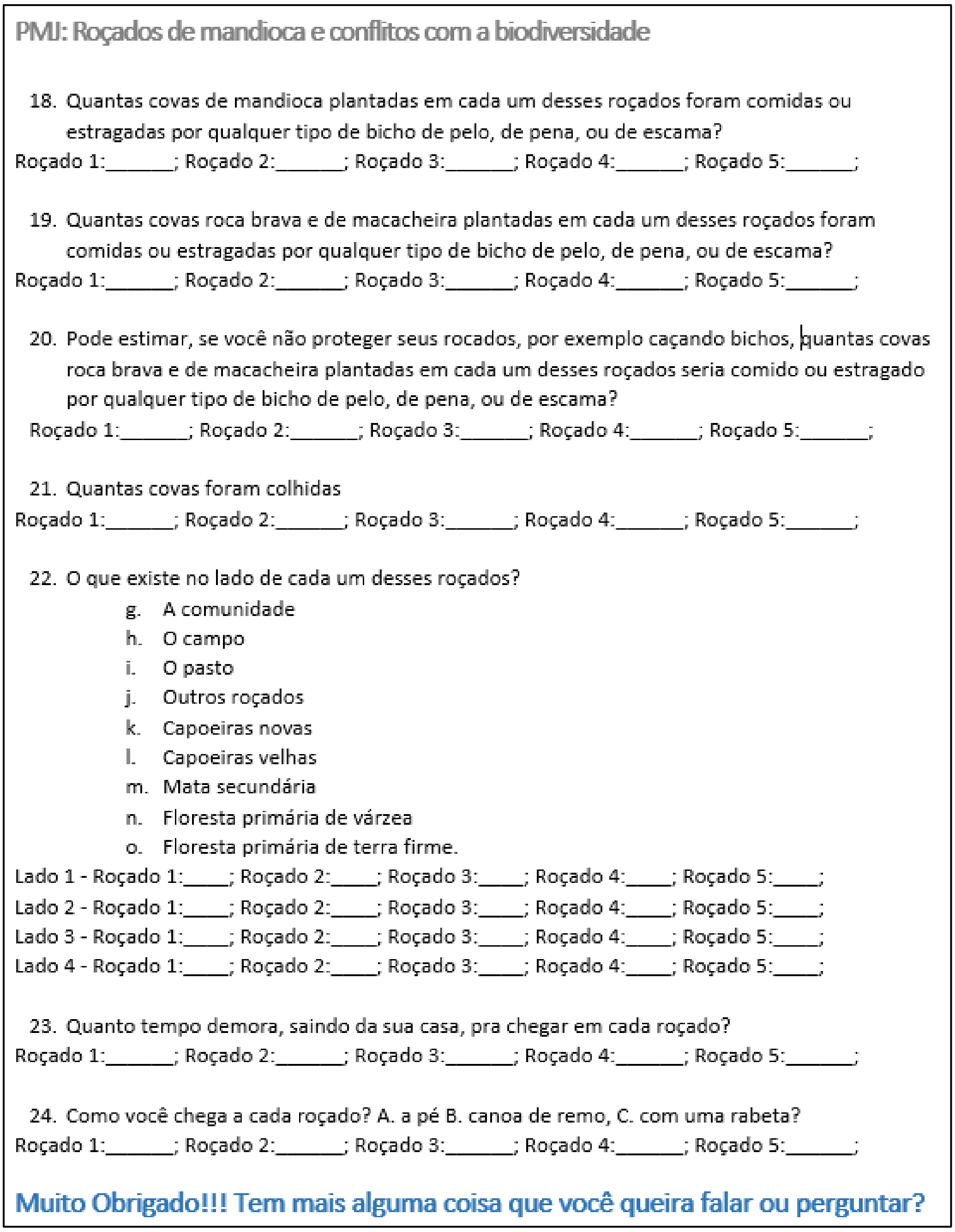
13. Quantos roçados o senhor possui?______________________________
14. Quantos meses atrás você começou a cada roçado? (a quanto tempo eles já estao "amadurando")
Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;

Por favor, dê uma resposta individual para cada um dos seus roçados plantados ou colhidos nos ultimos dois anos.

15. Quantas mil covas de mandioca foram plantadas em cada um desses roçados?
Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;

16. Quantas mil covas de roca brava e de macacheira foram plantadas em cada um desses roçados?
Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;

17. Quantas mil covas de mandioca foram perdidas pela alagação?
Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;



PMJ: Roçados de mandioca e conflitos com a biodiversidade

18. Quantas covas de mandioca plantadas em cada um desses roçados foram comidas ou estragadas por qualquer tipo de bicho de pelo, de pena, ou de escama?

Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;

19. Quantas covas roca brava e de macacheira plantadas em cada um desses roçados foram comidas ou estragadas por qualquer tipo de bicho de pelo, de pena, ou de escama?

Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;

20. Pode estimar, se você não proteger seus rocados, por exemplo caçando bichos, quantas covas roca brava e de macacheira plantadas em cada um desses roçados seria comido ou estragado por qualquer tipo de bicho de pelo, de pena, ou de escama?

Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;

21. Quantas covas foram colhidas

Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;

22. O que existe no lado de cada um desses roçados?

    g. A comunidade
    h. O campo
    i. O pasto
    j. Outros roçados
    k. Capoeiras novas
    l. Capoeiras velhas
    m. Mata secundária
    n. Floresta primária de várzea
    o. Floresta primária de terra firme.

Lado 1 - Roçado 1:____; Roçado 2:____; Roçado 3:____; Roçado 4:____; Roçado 5:____;
Lado 2 - Roçado 1:____; Roçado 2:____; Roçado 3:____; Roçado 4:____; Roçado 5:____;
Lado 3 - Roçado 1:____; Roçado 2:____; Roçado 3:____; Roçado 4:____; Roçado 5:____;
Lado 4 - Roçado 1:____; Roçado 2:____; Roçado 3:____; Roçado 4:____; Roçado 5:____;

23. Quanto tempo demora, saindo da sua casa, pra chegar em cada roçado?

Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;

24. Como você chega a cada roçado? A. a pé B. canoa de remo, C. com uma rabeta?

Roçado 1:______; Roçado 2:______; Roçado 3:______; Roçado 4:______; Roçado 5:______;

Muito Obrigado!!! Tem mais alguma coisa que você queira falar ou perguntar?

Appendix C - Methodological Details

1. For camera trap deployments, Bushnell Trophy-Cam, Trophy-Cam HD, and Reconyx HC500 Hyperfire models were used. Camera sensors were set to high sensitivity. They took 3 sequential burst photographs or 3 second video clips. A red light flash was used in very low light. Only deployments close (1.8km) to the agricultural mosaic were used for the analysis. Deployments were not made in *várzea*. Deployments outside contiguous primary forest were 25m from the habitat edge to control for edge effects. When deploying cameras, a community resident was employed to aid in the identification of suitable locations and determine the age of capoeiras since abandonment. Locations were not chosen to deliberately maximise detection (for example beneath fruiting trees), but conspicuous obstacles to detection were avoided. Bait was not used. Locations were chosen to have relatively flat ground, relatively unobscured by large trees/obstacles. Thin vegetation was cleared in a cone of 7 paces long by 7 paces wide in-front of the camera to permit detection and avoid detecting the movement of vegetation. Cameras were deployed at knee height, attached to trees. Walk-tests were performed to confirm correct positioning. Mothballs and tampons were put inside cameras along with batteries to repel insects and protect against humidity. A GPS waypoint was always taken. When cameras were removed, a note was made of any problems or malfunctions such as water ingress, insect attack, dislodgement or battery failure.
2. When summarising interview data, where single numeric responses were given, means were calculated. Where multiple unranked categorical responses were given, the number of responses per category were summed. Where multiple ranked categorical responses were given, a summed, rank-weighted score per category was calculated (∑ (∑ (ranked1) + ∑ (ranked2/2) + ∑ (ranked3/3)…)).
3. *Várzea* and habitat disturbance. For camera deployments, INPE PRODES, 2009, Hansen *et al.*, *(*2013) Global Forest Change (GFC) datasets were combined because though the GFC data is 30m rather than 120m pixel resolution and extends to 2014, it does not account for deforestation that occurred before 2000. Cells were reclassified into either deforested or not deforested. For GFC data, 50% deforested was used as the cut off. Deforested pixels were converted to polygons and merged. 500m was considered appropriate given the heterogeneous and fine-scale nature of the agricultural mosaics.
4. Distance-weighted variables for *várzea*, deforestation and local human population were calculated, but as these were not found to improve models, they were excluded from further analysis. Deforestation and *várzea*, polygons were separately converted to raster grid cells of 30m resolution to match the GFL dataset. The centre of each pixel was converted to a point. The distance from each camera to each point was calculated. This

was linear distance in the case of *várzea* and deforestation and transport distance in the case of households. Three weighted scores were calculated a) ∑ (1/distance) b) ∑ (1/(square root(distance))) c) ∑ (1/(natural log(distance))).

5. Respondents were asked what land use/land cover (from now “land cover”) bordered each of their *roçados*. Respondents were allowed up to four responses. Each land cover type was assigned a score (see table below) reflecting the degree of disturbance, with 10 indicating low disturbance contiguous primary forest and 1 indicating high disturbance homestead. Likewise, a *várzea* score was assigned, 1 indicating *várzea* and 0 indicating non-*várzea*. Scores per *roçado* were summed and divided by the number of responses, to give the mean “intactness” and “*várzea*” of the land cover surrounding the *roçado*.

Portuguese land cover/ land use description	English Equivalent	Intactness Score	*Várzea* Score
terra firme	primary forest unflooded	10	0
várzea	primary forest seasonally flooded	10	1
mata secundaria	secondary forest	8	0
capoeira velha	old abandoned roçado	6	0
capoeira nova	newly abandoned roçado	4	0
açaí	*acai* palm (*Euterpe oleracea*) plantation	3	0
pupunha	peach-palm (*Bactris gasipaes*) plantation	3	0
roçado	agricultural field	2	0
pasto	pasture	2	0
campo	field (for cattle or football)	2	0
comunidade	community	1	0

6. Data validation of households and deforestation. The table below compares the PRODES raster datasets between 2007 and 2013. The 2009 dataset was chosen because it has the smallest area of cloud and no-data and the largest area of data. It also corresponds closely in time to the 2007-2009 households census. The rural households points shapefile was aggregated at the level of census sector and district for the states of Amazonas, Para, Acre, Mato Grosso, Rondônia and Roraima, so that it could be compared to the IBGE 2007 rural population count. Similarly, the 2009 PRODES deforestation data was compared to the Hansen et al Global Forest Loss (GFL) dataset. The GFL “Year of gross forest cover loss event” raster layer was used so that loss until 2009 could be compared. In both cases, cells were reclassified into either deforested or not deforested. A subset of data for which there was both PRODES and GFL data was taken from the 00N_070W degree granule in the state of Amazonas. The data were aligned and aggregated (using ArcGIS tools “extract by mask” and “aggregate”) to a cell size of roughly 12500m, representing a 100 cell factor aggregation of the PRODES dataset. A 30km buffer was erased from this area to exclude edge effects caused by raster aggregation, leaving an area of analysis of 1,072,620 km². For both deforestation and households, a Spearman’s rank test was performed. The rural households point shapefile and the IBGE 2007 rural population census, were found to be strongly correlated. Aggregated by census sector, N = 8314, spearman value 0.69. Aggregated by district, N= 721, spearman value, 0.85. Likewise, the 2009 PRODES

dataset was found to be strongly correlated to the GFL dataset N=6854. Spearman’s Rho = 0.71. Note that the GFL data is at a finer, 30m resolution and does not appear to have cloud. It classifies pixels as percent deforested. It counts any vegetation above 5m in height as forest. It does not classify natural non-forest.

Yr	no data cells	data cells	cloud cells	cell size m	area per cell m²	no data km²	data km²	cloud km²
2013	516596930	555917128	80109142	90	8100	4184435	4502929	648884
2012	476386530	596127528	38370048	90	8100	3858731	4828633	310797
2011	475120657	598433411	36681641	90	8100	3848477	4847311	297121
2010	492497080	581056988	54072551	90	8100	3989226	4706562	437988
2009	262026591	341073034	15757106	120	14400	3773183	4911452	226902
2008	271926486	328258890	15962705	120	14400	3915741	4726928	229863
2007	279069068	321827326	20524032	120	14400	4018595	4634313	295546

7. For interviews, the number of households per community were calculated from three data sources 1) interviews conducted during this study 2) Projeto Medio Jurua interviews and 3) The Sustainable Forest Association (FAS) community census. Although our data is more recent, we were interviewing community members rather than conducting a population census. Mean values per community were used.
8. To calculate transport distance we used average speeds per transport type from Parry and Peres, 2015. Outboard motor (locally *rabeta*) 9km/h, un-motorised canoe 5km/h, on foot 4km/h. These mean speeds are confirmed by our fieldwork experience. Transport or Manhattan distance was considered a more appropriate metric than raw journey time because faster means of transport such as outboard motors have a higher associated cost to the user. Thus transport distance better reflects the difficulty/cost of accessing a *roçado*. In 3 out of 238 cases, no mode of transport was given by the respondent, so the mean transport speed for those communities was used
9. To convert data given per *roçado* into data per person per year, data for all the *roçados* planted by a given farmer in a given year were summed, then the average across all years was taken.
10. During fieldwork, and especially when conducting interviews, researchers acted respectfully towards local communities. Researchers took pains to integrate into community life wherever possible, asking for permission to work in communities, making short presentations explaining our work, participating in agricultural work, sharing meals, attending meetings, employing residents and sleeping in communities. When conducting interviews, we were open to respondent questions and suggestions and we emphasised that data would be kept anonymous and that it was perfectly acceptable to not respond

Chapter 4: Measuring local depletion of terrestrial game vertebrates by central-place hunters in rural Amazonia

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Abstract

The degree to which terrestrial vertebrate populations are depleted in tropical forests occupied by human communities has been the subject of an intense polarising debate that has important conservation implications. Conservation ecologists and practitioners are divided over the extent to which community-based subsistence offtake is compatible with ecologically functional populations of tropical forest game species. To quantify envelopes of depletion of forest vertebrates around human communities, we deployed a total of 383 camera trap stations and 78 quantitative interviews to survey the peri-community areas controlled by 60 semi-subsistence communities over a combined area of over 3.2 million hectares in the Médio Juruá and Uatumã regions of Central-Western Brazilian Amazonia. Camera trap data suggests that a select few harvest-sensitive species, including lowland tapir, are either repelled or depleted by human communities. Nocturnal and cathemeral species were detected relatively more frequently in disturbed areas close to communities, but individual species did not necessarily shift their activity patterns. This suggests that in our study areas, species composition, rather than behaviour, alters in response to anthropogenic pressure. The aggregate group biomass of all species was depressed in proximity to urban areas and accessible tributaries rather than in proximity to communities, suggesting urban-centric and anisotropic, rather than community-centric and isotropic depletion. Interview data, which better account for arboreal and rarely detected species, suggest that species traits, especially group size and body mass, mediate anthropogenic depletion/repulsion. Large-group-living and large-bodied species including lowland tapir, woolly monkey and white lipped peccary, are detected farther from communities as reported by experienced informants. Long-established communities in our study regions have not "emptied" the surrounding forests. Our study regions are however characterised by low human population density and plentiful alternative protein sources. They thus represent a best-case scenario, relative to low productivity regions of the upper Rio Negro and more densely settled regions of the Afrotropics and Asian tropics. Additionally, the unavoidable deployment of camera traps against a riparian productivity gradient, as well as the interview recall bias towards large-bodied species, likely make our assessment of depletion conservative.

4.1 Introduction

Conservationists from across the major tropical and subtropical regions have voiced concerns that vast tracts of apparently intact forest mask large-scale faunal extirpation (Bennett *et al*., 2000 - Malaysian Borneo; Hart, 2000 - DR Congo; Hill and Padwe, 2000 - Paraguay; Noss, 2000 - Central African Republic; Peres, 2000 - Brazilian Amazonia; Lahm, 2001 – Gabon; Madhusudan and Karanth, 2002 - Southern India; Datta *et al*., 2008 - Northeast India; Golden, 2009 – Madagascar; Steinmetz *et al*., 2013 – Thailand; Sreekar *et al*., 2015 - Southwest China). Where human communities extract tropical forest vertebrates, an “empty forest” scenario (Redford, 1992) may result, in which species larger than 2kg are virtually absent (Harrison, 2011). These defaunated forests may be subject to gradual degradation as the key functional roles played by megafauna are lost (Wright, 2003; Muller-Landau, 2007; Harrison *et al*., 2013). Although the importance of habitat fragmentation and degradation are recognised (Peres, 2001), hunting is often implicated as the main driver of defaunation (Fragoso, 1991) and heavily hunted sites have been shown to retain less than 20% of the crude vertebrate biomass of unhunted sites (Peres, 2000). Biodemographic models predict that the adoption of firearms over traditional weapons results in depletion envelopes for low fecundity, harvest-sensitive species, such as spider monkeys, around even low density, subsistence settlements in otherwise pristine remote forests (Levi *et al*., 2009).

It is argued that subsistence hunters operate as optimal foragers rather than conservationists (Hawkes *et al*., 1982; Alvard, 1993), always pursuing the most profitable prey irrespective of vulnerability. In multi-species prey assemblages, the persistence of harvest-insensitive species maintains the overall profitability of hunting, such that apparent competition drives vulnerable species to local extirpation (Clayton *et al*., 1997; Branch *et al*., 2013). Humans have been responsible for widespread faunal extinctions since prehistory (Martin, 1967; Bar-Oz *et al*., 2011). Apparent cases of past stable coexistence with sensitive prey species may be an incidental consequence of low local human population density and inefficient hunting technology (Low and Heinen, 1993), and are irrelevant to modern conservation given the widespread adoption of firearms (Mittermeier, 1987), increasing market integration (Holt *et al*., 2004) and human population growth even in protected areas (Peres, 2011).

Numerous measures of hunting sustainability have been proposed (Robinson and Redford, 1994; Milner-Gulland and Akçakaya, 2001) and in a wealth of studies, the actual hunting offtake has been shown to be unsustainable for several species (Peres, 1990 – Ateline primates; Altrichter, 2005 - white-lipped and Chacoan peccaries; Struebig *et al*., 2007 – flying foxes; Golden, 2009 – four species of lemur), resulting in areas of low prey biomass, low catch per unit effort, local extirpations and dramatically different prey offtake profiles (Wilkie and Carpenter, 1999; Fa *et al*., 2000; Corlett, 2007)

In some regions, commercial hunting to supply urban demand (the "bushmeat trade") is implicated as the key driver of overharvesting (Bowen-Jones and Pendry, 1999). In other regions, however, even subsistence hunting practiced by isolated households can severely depress local populations of harvest-sensitive species (Peres, 1990). Unsustainable hunting has been deemed an especially acute problem in tropical forests due to their global biodiversity importance (Gaston, 2000), intrinsically low wild-meat productivity (Milner-Gulland and Bennett, 2003), high projected population growth (Cincotta *et al*., 2000), and often insufficient resources to enforce conservation regulations (Peres and Terborgh, 1995).

In stark opposition, some authors have argued that subsistence hunting, as practiced in indigenous, sustainable use and extractive reserves, has little impact on populations of terrestrial game vertebrates (Schwartzman *et al*., 2000). Semi-subsistence and especially traditional communities often accumulate deep traditional ecological knowledge (Berkes *et al*., 1995) and a well-developed conservation ethic stemming from both spiritual beliefs and a history of resource management (Martinez, 1996; Berkes, 1999; Read *et al*., 2010). The long period of coexistence between humans and vertebrate game (Leeuwenberg and Robinson, 2000) implies long-term hunting sustainability. Far from being optimal foragers, subsistence hunters have complex culturally-mediated systems of resource utilisation rules and food taboos (McDonald, 1977; Da Silva, *et al*., 2005) including avoidance of vulnerable species, life-stages and seasons and the small and large-scale spatial rotation of hunting grounds (Berkes *et al*., 2000; van Vliet *et al*., 2010), all of which enable faunal recovery.

Several studies have reported that despite long-term hunting offtake levels that consistently exceed predicted maximum sustainable yields, game depletion is not evident through changes in bushmeat availability at markets, catch per unit effort, prey profiles, per capita consumption rates or mean prey weights (Alvard, *et al*., 1997; Ohl-Schacherer *et al*., 2007; van Vliet and Nasi, 2008). One explanation for this phenomenon is the replenishment through dispersal of hunted "sink" areas, by adjacent unhunted "source" areas (Novaro, *et al*., 2000). This calls into question the aforementioned claims that game species are typically overharvested within intensively hunted portions of village catchment areas. Furthermore, it is claimed that the density estimates used as evidence of hunting depletion are flawed. Hunted species are able to change their behaviour in response to persistent hunting and other anthropogenic disturbance, such that they become less detectable (Johns, 1985). Line-transect surveys therefore may fail to detect hunted species at hunted sites, whilst their presence is confirmed by tracks and signs (Fragoso *et al*., 2016).

Even in cases where densities of game species are reliably found to be depressed in proximity to semi-subsistence communities, it is argued that this is insufficient evidence to substantiate unsustainable local hunting. Firstly, as Robinson and Redford (1994) argue, depletion in itself does not entail a lack of sustainability. Offtake must by definition result in a spatio-temporally localised reduction in abundance and even where this depletion persists, yields may be maximised when a population is below its carrying capacity. Secondly, environmental factors may be responsible for complex population changes (Hill *et al*., 2003). Lastly, external influences such as (a) uncontrolled hunting practiced by illegal loggers, miners and commercial hunters from nearby urban areas (Parry *et al*, 2010), and (b) a reduction in available wildlife source areas due to the encroachment of commercial agriculture, may be driving game depletion.

These opposing views have important conservation implications. Some conservation biologists have argued for the need to prioritise the creation and enforcement of strictly protected areas that exclude humans and prevent hunting, in some of the world's most biodiverse tropical rainforests (Kramer *et al*., 1997; Brandon *et al*., 1998; Wilkie *et al*., 2011). Others have replied that the creation of large, strictly protected areas is (1) unethical, as they are either detrimental to the livelihoods of the world's poorest people (Norton-Griffiths and Southey, 1995), or displace semi-subsistence communities entirely (Geisler, 2003); (2) unnecessary because both standing forest (Porter-Bolland *et al*., 2012) and fauna are effectively conserved by communities (Ntiamoa-Baidu, 2008); and (3) counterproductive because (a) they damage relations with local communities who then become hostile to conservation (Nepal and Weber, 1995) and (b) they remove the very people best placed to defend biodiversity (Alcorn, 1993; Schwartzman *et al*., 2000), as local communities are relatively permanent and cost-effective deterrents of commercially motivated external agents of environmental degradation such as commercial hunters, logging companies and large-scale cattle ranchers, who have little incentive to conserve wildlife.

Here we contribute to this debate by assessing the degree of depletion of a range of neotropical forest vertebrates in to the vicinities of semi-subsistence communities and towns in Brazilian Amazonia using both camera trapping and interview surveys. We do not necessarily restrict the term "depletion" to demographic reduction via hunting offtake, though we consider this an important mechanism. As we do not have long-term hunting offtake data alongside species abundance data, even if we find that the abundance of certain species is depressed in proximity to human communities, we cannot thereby conclude that this is the result of demographic depletion. This could equally be the result of species dispersing away from communities. Therefore we use the term "depletion" for either depletion or repulsion. Equally, we cannot assess the long-term sustainability of hunting in these regions. Instead, we hope to provide a snapshot of the status of forest vertebrate populations.

We hypothesise that: (1) Harvest-sensitive species, including large-bodied species such as tapir, highly preferred game species such as white lipped peccary and low-lambda species such as Ateline primates, are depleted in proximity to semi subsistence communities in our study regions. This depletion will be evident through both (a) lower camera trap detection rates in proximity to communities, especially large communities and (b) larger interview-reported distances until sites of encounter relative to other species; (2) High-lambda, disturbance-tolerant species such as agoutis, which benefit from opportunities to raid agricultural plots, will be relatively more abundant in proximity to communities; (3) Nocturnal and cathemeral species, whose circadian activity patterns permit minimizing direct contact with humans, will be relatively more common in proximity to communities; (4) Cathemeral species, including brocket-deer and felids, will alter their behaviour in order to reduce human encounters, and will therefore exhibit higher detection rates at night when in proximity to communities; (5) The cumulative detected biomass of terrestrial vertebrates will be significantly depressed in proximity to communities; and (6) Overall detection rates will be lower in lower productivity black-water river basins, where the impact of hunting will be more severe.

To this end we make several key assumptions. Firstly, we assume that proximity to human settlements is a proxy for the intensity of hunting and other anthropogenic disturbance. This rests on the well supported observation that hunters behave as central place foragers (Sirén *et al*., 2004), such that hunting intensity declines from the centre of the community. Secondly, we assume that areas near human settlements are not otherwise intrinsically hostile to our study species. To the contrary, it is anticipated that human settlements were deliberately established in environmentally favourable locations. For example, we expect a higher human population density in areas allowing greater access to abundant natural resources as predicted by an ideal-free distribution. These resources include a higher soil fertility which mediates the density and species richness of nonvolant mammals across Amazonia (Emmons, 1984; Peres, 2008). Lastly, we assume that commercial hunting in our study regions represents a negligible fraction of total offtake and that we are not “missing” the most of the offtake by surveying subsistence hunting at the scale of local communities. This is plausible because (1) our study regions do not contain large urban populations and (2) culturally, hunted meat is not much sought by local urbanites (Projeto Médio Juruá, unpublished data).

4.2 Methods

4.2.1 Study Area

This study was carried out in the Médio Juruá and Uatumã regions of Western and Central Brazilian Amazonia (Fig. 4.1). The Médio Juruá study region covers an area of 1,637,008 ha and consists of 63.9% of primary unflooded (*terra firme*) forest, 30.0% of seasonally-flooded *várzea* forest, 4.4% of permanent water bodies, which include the Juruá River (the second-largest white-water tributary of the Amazon) and its tributaries and oxbow lakes, and 1.8% deforestation and 0.1% natural non-forest. Two sustainable-use reserve -- the Uacari Sustainable Development Reserve and the Médio Juruá Extractive Reserve -- jointly protect 42.3% of this landscape. The nearest towns are Carauari, which is 88 fluvial km downstream from the Médio Juruá Reserve and has a population of 4145 families, and Itamarati, which is 120 fluvial km upstream from the Uacari Reserve and has a population of 905 families.

The Uatumã study region covers an area of 1,601,704 ha and consists of 62.3% of undulating upland primary unflooded (*terra firme*) forest, 17.9% of primary low-lying and seasonally-flooded *igapo* forest, 11.1% permanent water bodies, which include the Uatumã River (which connects the Balbina reservoir to the Solimões River) and its main tributary the Jatapú River, 4.0% deforestation and 4.7% natural non-forest, which includes areas of *campina* and *campinarana* non-forest vegetation on oligotrophic soils. The Uatumã Sustainable Development Reserve legally protects 27.0% of this landscape. The nearest towns are Vila Balbina, which has a population of 420 families and is 66 fluvial km upstream of the reserve, and Sao Sebastião, Itapiranga and Urucará, with populations of 1214, 1345 and 2051 families, respectively, and are 37, 40, and 53 fluvial km downstream of the reserve, respectively.

Both regions are inhabited by *ribeirinhos* who are former rubber-tapper semi-subsistence communities of mixed-descent, with producer cooperatives and resource-management programs. Large-scale ecological and socioeconomic differences between the two study regions are due to river chemistry and proximity to Manaus, the largest city in the state of Amazonas. The Juruá region encompasses highly productive white-water floodplain ecosystems, whereas the Uatumã region encompasses less productive black-water ecosystems, potentially resulting in lower faunal biomass density at Uatumã. Secondly, the Juruá region is over five times farther from Manaus, which increases transaction costs and reduces market opportunities for Juruá inhabitants.

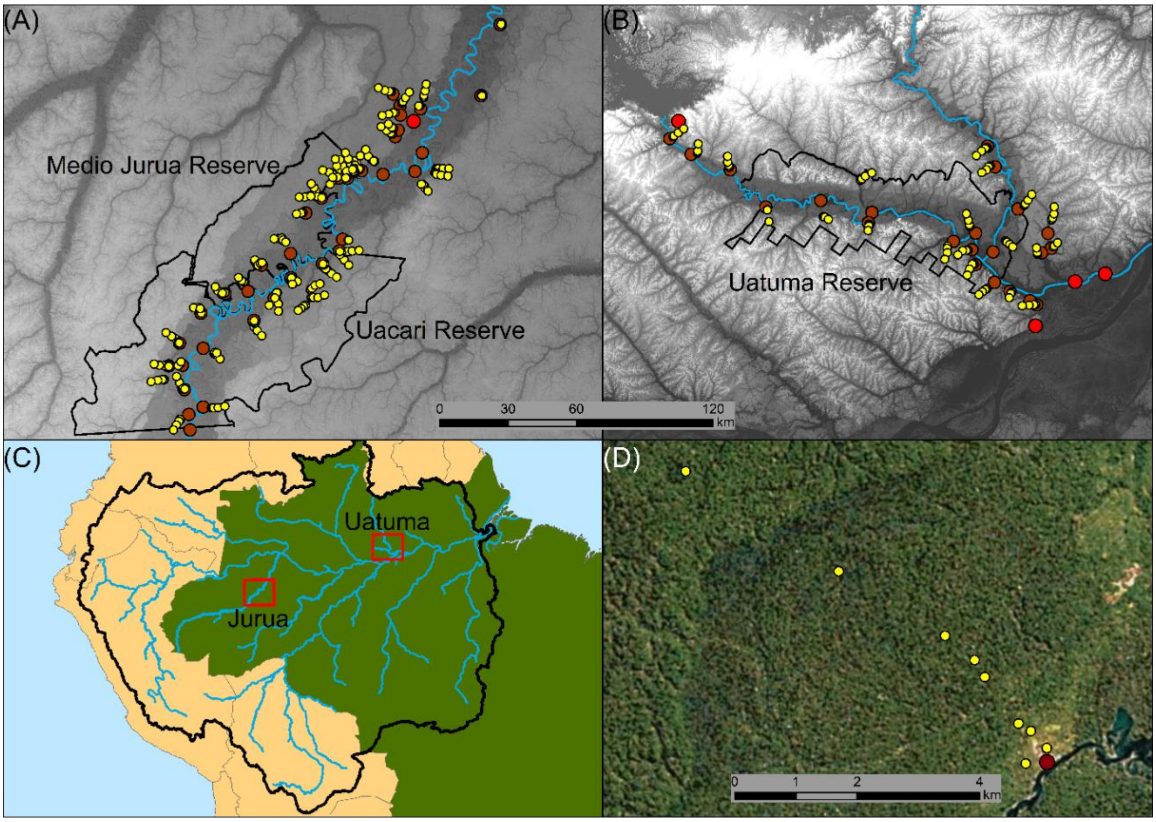

***Figure 4.1**: Geographic location of Juruá (A) and Uatumã (B) study regions within the Amazon basin (C) and the distribution of camera trap stations in an example community (D). Major rivers are represented as blue lines, towns as red circles, communities as brown circles and camera trap stations as yellow circles. Background in panels A and B, which are presented at the same scale, displays elevation, with darker shades indicating lower elevation. Sustainable use and extractive reserves are outlined in black. The Amazon basin (panel C) is outlined in black and the two study areas are outlined in red. In panel D, the four camera trap stations nearest one of the sampled communities were placed within the peri-community agricultural mosaic, whilst five other stations were within contiguous primary forest.*

4.2.2 Vertebrate species

For all species that were either the subject of interviews or reliably detected by camera traps, a series of species traits were compiled (Table 4.1). Species taxonomic relatedness was assessed (Appendix C). Values for species intrinsic rate of increase (lambda) were taken from Robinson and Redford (1991) and C.A. Peres (unpubl. data). Values for adult body mass per species was taken from Dunning, 1992, Carboneras, 1992, Baptista *et al*., 1997, Emmons and Feer, 1997, Nowak, 1999 and C.A. Peres (unpubl. data), with the mean of male and female adult body mass used for sexually dimorphic species. Where only a range of adult biomass was known for a given species, the median of the upper and lower limits was used. Values for mean group size per species were taken from the Projeto Médio Juruá faunal monitoring program (http://www.projetomediojurua.org/). Species were assigned an ordinal trophic score, with lower numbers indicating species feeding at a lower trophic level, on the basis of Wilman *et al*., 2014 and C.A. Peres (unpubl. data). Species were assigned a categorical activity pattern [diurnal, nocturnal or cathemeral], based on the camera trap detections (Appendix B). Species were assigned a score reflecting their propensity to enter agricultural plots, as reported by semi-subsistence agriculturalists in the Juruá region (for more details see Chapter 3). Lastly, species were assigned a region-specific score reflecting the frequency with which they are hunted, as reported by respondents in both the Juruá and Uatumã regions.

4.2.3 Camera Trapping

Data collection took place between 2013 and 2015, between April and August to avoid the period of heaviest rainfall during which cameras are often damaged. A total of 383 camera-trap deployments (hereafter, CTD) were conducted according to a standardised deployment protocol (Appendix A1). Mean functioning camera-trap-nights (CTN) per deployment was 31.4 ± 0.4 CTNs. Mean nearest neighbour distance between deployments was 962.1 ± 47.4 m, although camera-traps were deployed along a ~852-km nonlinear distance along the Juruá, Uatumã and Jatapú Rivers.

Camera traps were deployed both in proximity to the peri-community agricultural mosaic and in contiguous primary *terra firme* forest along transects leading away from local communities. In the Juruá region, 132 camera-traps were deployed in the peri-community agricultural mosaic, stratified across several landscape-scale habitat types ranging from large tracts of undisturbed primary contiguous forest, to homestead areas in close proximity to community households. Due to time constraints, it was not possible to replicate the agricultural deployments in the Uatumã region.

In both the Juruá and Uatumã regions, the remaining camera trap deployments were carried out along 6-km transects starting at an area of contiguous primary *terra firme* forest nearest the community, and radiating away from the community. Waypoints were taken at the edge of contiguous primary forest and cameras were deployed at intervals of 50m, 350m, 1000m, 3000m and 6000m Euclidean distance along the transect, which can be converted to a near-exact log-linear scale (Pearson r = 0.983).

For each deployment, the following data were recorded: (1) identity and coordinates of the nearest local community; (2) coordinates of the camera-trap station; (3) date and time of deployment and removal; (4) in case of malfunction; date and time of last photograph; (5) habitat type; and (6) if deployed in secondary forest, age (yrs) since abandonment as determined by community residents.

Images were edited to improve contrast and aid species identification, and separated into deployment subfolders corresponding to ecospecies. Congeners from different study regions such as trumpeters (*Psophia leucoptera* and *Psophia crepitans*) were treated as a single ecospecies. Closely related species that could not be consistently identified to species level, such as *Dasypus kappleri* and *Dasypus novemcinctus*, were grouped into a single ecospecies. Images of domestic animals, humans, small passerines, primates, bats, small lizards, vultures, insects, were excluded from further analysis. We extracted all EXIF metadata including date and time from subfolders using the camtrapR package within R (Niedballa *et al*., 2016) and Picture Information Extractor software (Picmeta Systems, 2016). Data were compared with field notes and date/time were corrected where necessary. Images of conspecifics at any given deployment >30 min apart were defined as independent detections, which were then summed at the scale of camera-traps.

The different number of functioning camera trap nights per camera were accounted for as follows. When species detections were the response variable in statistical models, the number of functioning camera trap nights was designated as a model offset variable. Where species detections are compared graphically, or in analyses where offsets could not be used, detections were divided by the number of functioning CTNs to derive an abundance metric.

In the case of ambiguous images for which a subject could only be identified to a broader ecospecies, a deployment-specific detection rate was calculated for each ecospecies sub-category, and then used to apportion detections between sub-categories. If that deployment included no photographs that could be reliably identified to either sub-category, then the overall detection rate for all deployments was used.

Species-specific camera trapping detections were multiplied by the species body mass to provide an approximate metric of detected individual biomass. Because camera traps may fail to detect some group members, we simply defined detections as a single adult of undetermined sex. In order to account for species differences in group size, this individual biomass estimate was multiplied by the mean group size to give the detected group biomass per species per camera trap deployment.

Several groupings and weightings of detected group biomass were created per camera trap deployment as follows (1) All – the summed group biomass of all species; (2) All.nq - the summed group biomass of all species, except for the large-group-living white-lipped peccaries (whose detected biomass was extremely clumped) to determine if it this species had a disproportionate effect on our results); (3) Bin.hunt – the summed group biomass of all species identified in interviews as hunted (see Methods below); (4) Bin.hunt.nq - the summed group biomass of all species identified in interviews as hunted, except for white lipped peccaries; (5) Bin.huntpers - the summed group biomass of all species either identified in interviews as hunted, or livestock predators including felids, mustelids and opossums; (6) Binhuntpers.nq - the summed group biomass of all species either identified in interviews as hunted, or livestock predators including felids, mustelids and opossums, with the except for white lipped peccaries; (7) Bin.pers - the summed group biomass of all species identified in interviews as livestock predators including felids, mustelids and opossums; (8) Bin.unpers - the summed group biomass of all species neither identified as hunted nor as livestock predators; (9) Hw - the summed group biomass of all species, weighted by the region-specific frequency with which they were hunted, derived from interviews; (10) –Hw.nq - the summed group biomass of all species, weighted by the region-specific frequency with which they were hunted, derived from interviews, except for white lipped peccaries; (11) Rw - the summed group biomass of all species, weighted by their propensity to enter agricultural plots as reported in agricultural interviews; and (12) Rw.nq - the summed group biomass of all species, weighted by their propensity to enter agricultural plots as reported in agricultural interviews, except for white lipped peccaries.

4.2.4 Local Interviews

Interviewees were resident in their respective communities for an average of 20 ± 1.5 years. When asked how frequently they entered the forest, the 54% responded “weekly”, 16% “monthly”, 13.5% “annually”, 10.1% “daily” and 5.4% “weekly/monthly”. Making the simplifying assumption that all of our 151 respondents have worked in the forest for eight hours, once a week for the past 20 years, these interviews represent a combined total of 143 interviewee-years of experience.

Interviews were conducted in Portuguese by the authors and without the aid of translators. Interviews were recorded using a structured questionnaire and a dictaphone, and cross-validated for accuracy. Interviewees were reassured that data would be kept anonymous and confidential, and were not paid, but some were participating in paid work such as camera trapping at the time of interviews. A total of 78 interviews were conducted, with a total of 151 respondents at 59 local communities or urban neighbourhoods (hereafter, *communities*). Interview topics included encounters with forest vertebrate fauna, household-scale livelihoods, diet, hunting, farming, crop raiding, and other human-wildlife conflicts. For methods relating to interviews that focussed exclusively on agricultural plots and crop raiders, see Chapter 3.

Respondents were asked to estimate the time it would take, from leaving their home, to reach any given site at which a given species (or its tracks, scats and other perishable signs) could normally be encountered and the modes of transport used. Where respondents were unable to judge this, they were asked for the location of the most recent detection of that species or its perishable signs. Where a range of possible travel times were reported (several respondents explained that for a given species, encounter time was highly variable), an average was used, but where separate times were reported for direct encounters and encounters with signs, the lower of the two estimates was used. This partly accounted for highly elusive species, such as large felids, which respondents reported to be present, but were often undetected. In rare cases where responses were given in days rather than hours, a day was assumed to be eight travel hours. We differentiated between respondents who reported with certainty that a given species had not been encountered at all in the vicinity of the community and those who said they did not know how far one would need to travel in order to encounter a given species. In the former case, we assumed that reported absences reflected a lack of detections within 24 travel hours from the community. In the latter case, we did not record an encounter distance, because we assumed that this threshold could not be confidently estimated by the respondent, perhaps through lack of experience in identifying tracks and other signs of a given species. The Manhattan distance to a species encounter was calculated using the transport time and mode of transport reported from interviews, and average transport velocity (Parry and Peres, 2015; Appendix A3).

4.2.5 Spatial variables

The distance between camera trap deployments and the nearest community and town, as well as between interviewed communities and the nearest town, was calculated as follows. A GPS waypoint was recorded at the centre of all communities including those interviewed or in proximity to our camera deployments. A transport network accounting for all main rivers, tributaries, known navigable perennial streams, roads and known tracks in the vicinity of all surveyed communities and camera deployments was constructed from GPS track-logs taken over successive fieldwork years. We used the Network Analyst to calculate the Manhattan or "transport" distance between deployments, communities and towns across both study regions. Having identified the community/town with the shortest Manhattan distance to a given camera/interviewed community, we then calculated the Euclidean distance between them, giving us a "hybrid" distance. Raw Euclidean distances were deemed inadequate because it does not account for the barriers and enablers that influence human travel across landscapes. Likewise raw transport distance was not used because forest vertebrates using the landscape are not hindered or enabled by landscape features such as rivers in the same way as humans. Instead an intermediate measure was preferred.

The number of households per community was recorded using: (1) interviews conducted during this study; (2) Projeto Médio Juruá interviews; and (3) The Sustainable Forest Association (FAS) community census data. Although our data are more recent, we were interviewing community members rather than conducting a population census. Mean values per community were used. The number of households per urban centre was calculated using IBGE (2007) census data.

Hybrid distance and urban population were combined into a single variable, the urban proximity score. This was calculated as the urban population, divided by the square-root of the hybrid distance to a given community or camera-trap deployment. We have previously devised and used more complex urban proximity indices (see Chapter 2), but our study landscape in this chapter is simpler and alternative urban proximity indices are highly correlated.

The bulk of our camera-trap deployments were in contiguous primary forest. It was therefore not possible to investigate habitat effects in detail. Instead, we focussed on the proportion of primary forest in proximity to cameras. For each CTD, the area of primary forest (including both floodplain *várzea* forest and upland *terra firme* forest) within a 500-m buffer was calculated. Data from INPE PRODES (2009), Global Forest Change (GFC: Hansen *et al*., 2013), RADAMBRASIL (Veloso, 1982), and the Instituto de Conservação e Desenvolvimento Sustentável Amazonas (IDESAM) were used in order to exclude deforested areas, permanent water bodies and natural non-forest vegetation, including white-sand *campina* and *campinarana*, from the 500-m buffers. *Várzea* and *terra firme* forest were not treated as separate variables because they were strongly correlated with one another and with relative elevation. PRODES and GFC datasets were cross-validated (see Chapter 2 for methods).

The elevation of each CTD relative to the adjacent main river or stream was calculated following Rennó *et al* (2008). Raw elevation is inappropriate due to landscape-wide elevational gradients. There are 24m and 22m elevational differences between the extremes of our Juruá and Uatumã study landscapes, respectively and a roughly 65m elevational difference between study regions. To calculate the elevation of the river in proximity to each deployment, a point shapefile of camera deployments was snapped to a polyline of the main rivers. A 500-m buffer around each snapped point was then created and the lowest elevation within the buffer was used. The buffer was used to ensure that the true elevation of the river would be captured, rather than the nearby banks. The relative elevation per CTD was the elevational difference between the camera itself and the corresponding point on the main river. A map of perennial streams was created, using data from both the IBGE (2008) “hidro tot linha” shapefile and the Hydrosheds hydrographic dataset (Lehner and Grill, 2013a). The Euclidean distance between each CTD and the nearest perennial stream was then calculated. All spatial variables were extracted in ArcGIS (version 10.3)

4.2.6 Statistical Analysis

All statistical analyses were conducted in R. Collinearity between independent variables was tested for using Spearman’s Rank, Kruskal-Wallis and Wilcoxon Rank Sum tests. Where explanatory variables had bivariate Rho >0.70 or p <0.05, they were modelled separately. Data distributions and relationships were inspected using histograms. For count data, Poisson models were attempted and where overdispersion was revealed, Negative Binomial models were used. For distance-to-encounter data, Gaussian (using both identity and log links) and Gamma models were tested and inspected for model fits. In order to avoid creating over-fitted, ecologically meaningless models, we included a relatively small number of variables, all of which could plausibly impact our dependent variables. Variables were scaled to enable models to converge and aid variable effect size comparisons.

The ‘best’ models were selected based on their Akaike's weights (wAICc) and the ΔAICc, corrected for small sample sizes. We considered models with ΔAICc<2.0 and wAICc>0.1 as equally plausible to explain observed patterns (Burnham & Anderson, 2003). Where multiple plausible models were retained, they were weighted and averaged using the *model.avg* function in the R package *MuMIn*. Because extracting odds ratios from averaged models is problematic, we report coefficients and adjusted standard errors along with p-values per explanatory variable, to aid interpretation. We appreciate that "P-values are not part of the information theoretic paradigm" (Anderson and Burnham, 2002) and that reporting them alongside models selected on information-theoretic grounds is discouraged. Nonetheless, information-theoretic approaches can result in overly complex models (Link and Barker, 2006) and the mere fact that a "best" model has been specified, does not guarantee that any of the retained independent variables strongly influence the dependent variable.

Wilcoxon rank sum tests showed that camera-trap stations and interviewed communities inside protected areas had significantly lower urban proximity scores than those outside of protected areas ($p < 0.01$ and < 0.001 respectively). Further Wilcoxon tests also showed that community size, urban proximity score, proportion of primary forest, distance to stream, and elevation all differed significantly by region ($p <0.05$, < 0.001, <0.05, <0.01, and < 0.001, respectively). Protected status and study region were therefore not included as explanatory variables in multivariate models. REGION was however included as a nested random effect in negative binomial generalized linear mixed effects models (GLMMs). To separately test the effects of protection and study region on detection rates, the number of detections of every species at every camera was modelled as the dependent variable in a negative binomial GLMM with sampling effort (functioning CTNs) as an offset, protected status or region as explanatory variables and both species and camera IDs as random effects. To test for the effect of protection on overall biomass, the detected group biomass for all species, summed per camera, was modelled as the dependent variable in a negative binomial GLMM with sampling effort as an offset, protected status or region as explanatory variables and camera ID as a random effect. To further test the effect of protection and study region on depletion envelopes around communities, detection distances of each species reported from each interview was modelled as the dependent variable in a Gamma GLMM with protected status or region as explanatory variables and both species and community ID as random effects.

To investigate the degree of depletion of our study species, negative binomial GLMMs were created for (a) independent detections of each species detected at > 10 camera trap stations; (b) the total number of detections of all species per camera; and (c) each of the 12 biomass groupings described above. In each case, the log of the number of functioning CTNs was specified as an offset variable and study region and community ID were designated as nested random effects. The following anthropogenic and ecological variables as described above were included as fixed effects – the distance to the nearest community (COM.DIST), population of the nearest community (COM.POP), the urban proximity score (TOWN), the percentage of primary forest (PRIMARY), the distance to the nearest perennial stream (STREAM), and relative elevation (ELEV). An interaction between the variables COM.DIST and COM.POP was initially specified, but it was removed as it failed to produce stronger models. Where models did not converge, they were simplified by first removing REGION from the nested random effect, and then by removing the fixed effects with the lowest bivariate correlation with the dependent variable in question.

To investigate the impact of anthropogenic disturbance on the activity patterns of our study species, the first photograph of every independent detection per species was assigned a temporal period, with daytime specified as between 06:00h and 18:00h and night-time the converse. The number of nocturnal and diurnal detections per species, and for all species combined, were summed per camera. Negative binomial GLMMs were created (a) for every species detected at > 10 camera trap stations; and (b) for all species detected. GLMMs were structured as described above, except that the log of the total number of detections was specified as an offset.

In order to determine if nocturnal and cathemeral species were relatively more common in areas of high anthropogenic disturbance, independent detections were categorised as of either diurnal or nocturnal/cathemeral species. The number of independent detections of non-diurnal species were summed per camera and treated as the response variable in a multivariate negative binomial GLMM, with the log of the total number of independent detections per camera as an offset, and the community ID and region as nested random effects.

Lastly, Gamma GLMMs were used to assess the relative importance of both species traits and anthropogenic variables on the detection distances reported during interviews. Data were disaggregated such that the reported detection distance for every species from every interview was used as the dependent variable. To account for both data nestedness and phylogenetic relatedness, both species identity nested within taxonomic family (Appendix C) and community identity, were specified as random effects. Explanatory variables included simultaneously in the initial global model were the urban proximity score, community size, the region-specific hunting score, species intrinsic rate of increase, body mass, group size, trophic score and activity category. The agricultural score was excluded because it co-varied with the hunting score. Activity category and trophic score were subsequently excluded to allow models to converge.

4.3 Results

4.3.1 Species detections at camera trap stations

A total of 38 vertebrate species were either the subject of interviews, reliably detected by camera traps, or both (Table 4.1). A total of 34 taxa were reliably detected by camera traps (Fig. 4.2). The 15 most frequently detected species accounted for >90% of all detections. In the Uatumã region, only 25 taxa were reliably detected. The following taxa were detected in Juruá but not Uatumã: Atelocynus microtis, Procyon cancrivorus, Tayassu pecari, Sciurus ignitus, Sciurus spadiceus, Leptotila spp, Odontophorus spp Ortalis guttata and Penelope jacquacu. Considering only the 10 most frequently detected species, *Cuniculus paca* was detected over twice as frequently in the Juruá than the Uatumã region, and *Myoprocta spp* and *Pecari tajacu* were both detected more than three times as frequently in the Uatumã region than the Juruá region.

When species are ranked according to the detected group biomass, the 10 top-ranking species accounted for >90% of the total detected biomass. Between regions, the overall detected grouped biomass raking is similar except for (1) *Tayassu pecari*, which accounted for the highest detected biomass in Juruá but was not detected in Uatumã; (2) *Cuniculus paca* and *Myrmecophaga tridactyla*, which had detected biomass twice as high in the Juruá than the Uatumã; and (3) *Pecari tajacu*, the detected biomass of which was over three times as high in Uatumã than in Juruá.

Table 4.1 – Study species reliably detected by camera traps or the subject of interviews and their key traits. Hunt.Jur and Hunt.Uat are scores of the frequency with which a given species is hunted, as determined by interviews with residents of both the Juruá and Uatumã regions.

Species binomial	English name	Species code	dataset	lambda	Body mass	Group size	Agricultural score	Hunt Jur	Hunt Uat	trophic number	activity pattern
Alouatta spp	howler monkey	Alou.sp	interview	1.17	6500	6.2	0	4.1	0	2	diurnal
Ateles spp	spider monkey	Atel.sp	interview	1.08	9020	11.7	0	0	0	3	diurnal
Atelocynus microtis	short eared dog	Atel.mi	camera	1.15	7750	1.2	0	0	0	5.5	diurnal
Chelonoidis spp	red/yellow footed tortoise	Chel.sp	interview	2.5	4580	1.2	0	0	0.8	2	diurnal
Crypturellus spp	small tinamou	Cryp.sp	both	1.9	420	1.4	1.2	2.3	0	3	diurnal
Cuniculus paca	lowland paca	Cuni.pa	both	1.95	9500	1	13.3	14.5	31.8	3	nocturnal
Dasyprocta spp	agouti	Dasy.sp	both	3	4500	1.2	23.3	8.1	17.8	3	diurnal
Didelphis marsupialis	common opossum	Dide.ma	camera	5	1087.5	1	0	0	0	4	nocturnal
Echimyidae spp	spiny rat	Echi.sp	camera	5	560	1	0.8	0	0	3	nocturnal
Eira barbara	tayra	Eira.ba	camera	1.32	4850	1.3	1.4	0	0	5.5	diurnal
Lagothrix spp	woolly monkey	Lago.sp	interview	1.12	8710	19.6	0	1.3	0	3	diurnal
Leopardus pardalis	ocelot	Leop.pa	camera	1.58	15000	1.3	0.1	0	0	6	cathemeral
Leopardus wiedii	margay	Leop.wi	camera	1.58	6000	1	0.5	0	0	6	cathemeral
Leptotila spp	dove	Lept.sp	camera	2	149	1.3	1.7	0	0	3	diurnal
Mazama americana	red brocket deer	Maza.am	both	1.42	30000	1.1	19.4	8.3	4.8	2	cathemeral
Mazama nemorivaga	grey brocket deer	Maza.ne	both	1.61	18000	1.2	0	1.3	2.9	2	cathemeral
Metachirus spp	four-eyed opossum	Meta.sp	camera	5.2	390	1	0	0	0	4	nocturnal
Mitu or Crax spp	currasow	Mitu.Cr	both	1.465	3000	1.6	2.3	8.3	7.9	3	diurnal
Myoprocta spp	acouchy	Myop.sp	camera	3	750	1	0.1	0	0	3	diurnal
Myrmecophaga tridactyla	giant anteater	Myrm.tr	both	1.7	30500	1.2	0.5	0	0	5	diurnal
Nasua nasua	south American coati	Nasu.na	camera	1.26	5100	11.9	0	0	0	5.5	diurnal
Nonspecific Cingulata small	small armadillo	Nons.Ci	camera	1.905	30000	1	9.3	2.8	8.1	5	nocturnal
Odontophorus spp	wood quail	Odon.sp	camera	1.8	310	5.4	0	0	0	3	diurnal
Ortalis guttata	speckled chachalaca	Orta.gu	camera	1.76	1200	5	0.5	0	0	3	diurnal
Panthera onca	jaguar	Pant.on	both	1.26	80000	1.4	1.7	0	0	6	cathemeral
Pecari tajacu	collared peccary	Peca.ta	both	2.01	25000	4.9	15.9	16.5	15	4	diurnal
Penelope jacquacu	spix's guan	Pene.ja	camera	1.491	1280	4.9	0.1	0.3	0.5	3	diurnal

Species binomial	English name	Species code	dataset	lambda	Body mass	Group size	Agricultural score	Hunt Jur	Hunt Uat	trophic number	activity pattern
Priodontes maximus	giant armadillo	Prio.ma	both	1.8	6000	1.2	1.6	0	0	5	nocturnal
Procyon cancrivorus	crab-eating raccoon	Proc.ca	camera	1.39	5400	1	0	0	0	5.5	nocturnal
Psophia spp	trumpeter	Psop.sp	camera	1.3	1200	5.8	0	0	0	4	diurnal
Puma concolor	puma	Puma.co	both	1.36	45000	1.1	1.2	0	0	6	cathemeral
Puma yagouaroundi	jaguarundi	Puma.ya	camera	1.58	8000	1	0	0	0	6	diurnal
Sciurus ignitus	Bolivian squirrel	Sciu.ig	camera	3.6	700	1.2	0	0	0	3	diurnal
Sciurus spadiceus	South American red squirrel	Sciu.sp	camera	3.5	1200	1.4	0	0	0	3	diurnal
Tamandua tetradactyla	southern tamandua	Tama.te	camera	1.62	4500	1.1	0	0	0	4.5	nocturnal
Tapirus terrestris	Brazilian tapir	Tapi.te	both	1.22	160000	1.2	3.1	5.4	5.3	2	nocturnal
Tayassu pecari	white lipped peccary	Taya.pe	both	1.58	32000	68.3	0.2	21.1	1.9	4	cathemeral
Tinamus spp	large tinamou	Tina.sp	both	1.5	1200	1.3	1.2	4.7	2.2	3	diurnal

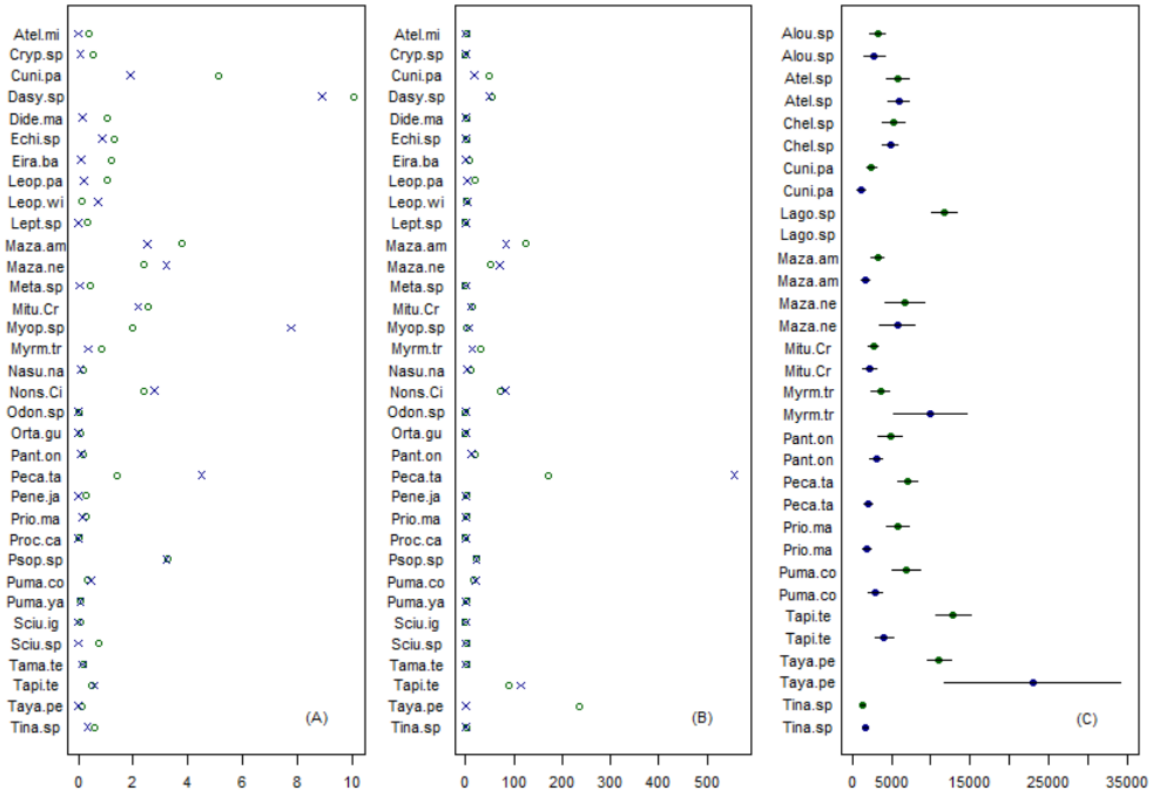

Figure 4.2: *Species detections from camera trap and local interview data. Species codes are indicated to the left of each panel. Species are arranged alphabetically by species code in all panels. Panel A shows the number of camera trap detections per 100 camera trap nights. Panel B shows the group biomass (kg) detected per 100 camera trap nights. Panel C shows the mean interview-reported detection distance (m) and standard errors. In Panels A and B, detections from the Juruá and Uatumã regions are indicated by open green circles and blue crosses, respectively, whereas in Panel C, Juruá and Uatumã detections are indicated by green and blue closed circles, respectively.*

4.3.2 Group biomass and species-specific models

Models of summed detections and of detected grouped biomass are highly consistent (Fig. 4.3 and Appendix D). For all grouped-detection models that include hunted species, whether they were weighted or unweighted by hunting preference or propensity to enter agricultural plots, and whether or not they included white-lipped peccary, detected biomass and total detections were significantly depressed in proximity to urban areas. Areas close to perennial streams also had lower detected grouped biomass, whereas summed detections (not accounting for biomass) were lower in areas close to communities with a low proportion of primary forest. In contrast, the biomass of species that are neither hunted nor persecuted was most strongly influenced by habitat, with a higher biomass detected in primary forest. In single-species detection models (Fig. 4.4), no single explanatory variable significantly influenced the detection of all species. Species response instead appear to be highly idiosyncratic.

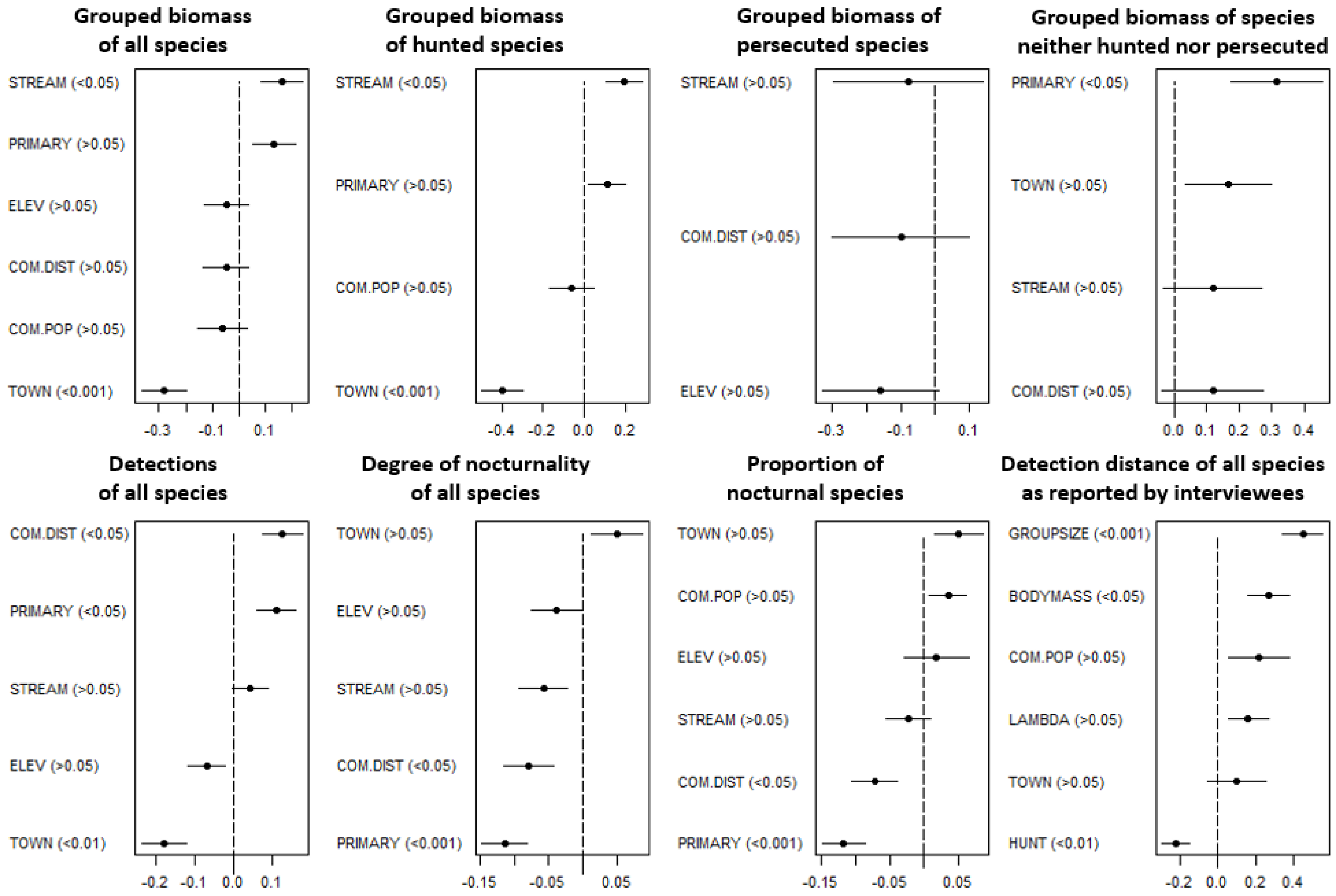

***Figure 4.3**: Explanatory variables retained in GLMMs investigating anthropogenic impacts on species abundance and activity patterns utilising camera trap and interview data. Explanatory variables and associated P-values are reported to the left of each panel. Coefficients and adjusted standard errors are represented by black circles with black lines.*

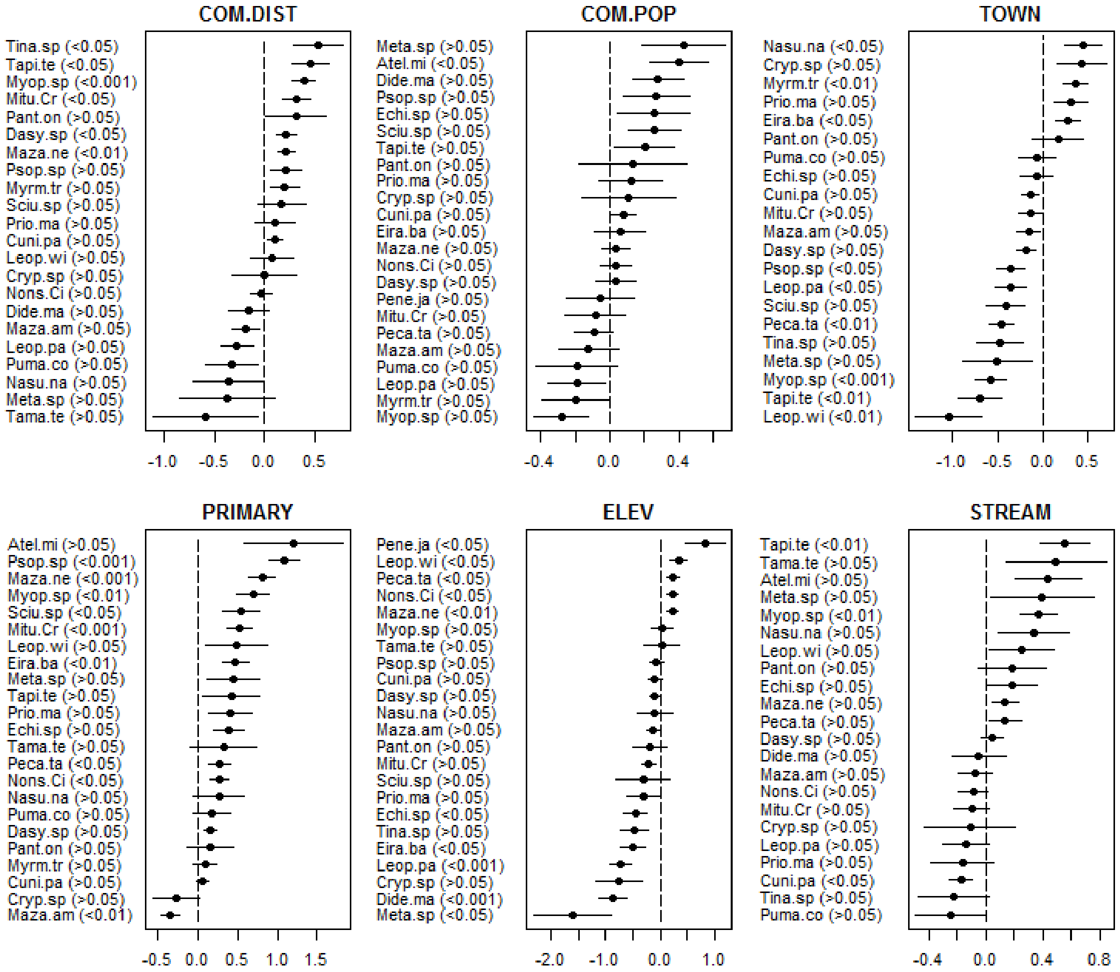

***Figure 4.4**: Coefficients and adjusted standard errors of the explanatory variables retained in GLMMs investigating camera trap detection rates of individual species. Species codes and associated p-values are shown to the left of each panel, ranked by coefficient, from highest to lowest.*

4.3.3 Species activity patterns

Most of our study species are diurnal (Table 4.1 and Appendix B), a smaller number are nocturnal, and the minority are cathemeral. Models suggest (Fig. 4.3) that in areas in proximity to communities with a low proportion of primary forest (a) pooled detections of the entire species assemblage were significantly more nocturnal; and (b) the proportion of nocturnal and cathemeral species detected was relatively higher. However, single-species activity models (Appendix E) were weak, generally with no single variable significantly predicting the proportion of nocturnal detections, except for grey brocket deer and collared peccary. The former was detected relatively more frequently at night when close to communities, whilst the latter was detected more frequently at night in areas with a low proportion of primary forest and at higher elevation.

4.3.4 Local interviews

In the Juruá and Uatumã regions over 89% and 91% of respondents, respectively, deemed wild-caught fish a more important food source than game meat, whilst just over 4% in both regions considered them equally important. In the Juruá region, the most important livelihood activities were considered to be agriculture (mainly manioc, but also bananas, maize, squash, watermelon and pineapple), fishing (both for subsistence and as part of a fisheries management program), social welfare programs (including Bolsa Familia, Bolsa Verde and Bolsa Floresta) , extractivism (including rubber-tapping and other nontimber resource harvesting, including *Euterpe oleracea* (locally *açaí*), *Astrocaryum murumuru* (*murumuru*), *Carapa guianensis* (*andiroba*), *Copaifera multijuga* oleoresin (*copaiba*), and *Heteropsis flexuosa* (*cipó titica*)), hunting (subsistence only), wage labour, timber (including harvesting and carpentry) and livestock (including cattle, pigs and chickens). These represented 43.0, 19.9, 14.1, 14.0, 3.9, 3.8, 1.2 and 0.2% of the summed weighted scores, respectively. In the Uatumã region, the most important livelihood activities were considered to be agriculture, salaried work, social welfare programs, extractivism, timber, livestock, fishing and hunting, representing 55.4, 10.6, 8.2, 6.7, 6.4, 6.2, 5.5 and 0.9% of the summed weighted scores respectively.

Our interviews gathered detection data for a total of 16 species, one of which (*Lagothrix spp*) does not occur in the Uatumã region. In models using all interview responses for all species, the variables that most strongly influenced reported detection distances were species traits, rather than anthropogenic landscape metrics such as proximity to an urban centre or size of the nearby community. Large-bodied species that form large groups and that are less preferred by hunters, are reportedly detected the farthest away. Although there was significant overlap between the species from the different landscapes identified as hunted, the species rankings differed (Table 4.1).

Camera trap detection rates inside protected areas were significantly higher and associated with a higher overall group biomass than those outside protected areas ($p < 0.05$ in both cases). However, respondents outside protected areas did not necessarily report significantly longer overall encounter distances than respondents inside protected areas ($p = 0.06$). Study region had no significant effect on overall detections, detected biomass or encounter distance ($p > 0.05$ in all cases).

4.4 Discussion

Concerns that tropical forest reserves legally occupied by human communities are inevitably “emptied” of large-bodied terrestrial forest vertebrates, are not borne out in our study regions, which retain large game populations, despite harbouring many long-established semi-subsistence communities. Nonetheless, our camera trap and interview data support evidence that (a) landscape-scale human population density depresses the detectable aggregate biomass of the entire vertebrate species assemblage; (b) nocturnal species are relatively more prevalent in areas near communities; and (c) large-group-living species, that are disproportionately affected by hunting, are virtually absent from areas in close proximity to communities. Our initial hypothesis that the detection rate of large-bodied, low-lambda species would be significantly depressed in proximity to semi-subsistence communities cannot be falsified, but as currently stated may be oversimplified.

4.4.1 Models of species detections, group biomass, activity patterns and encounter distance

In single-species models, a select few species met our expectations. The largest-bodied terrestrial mammal, tapir, was negatively impacted by both local communities and urban areas. Grey brocket deer, a shy selective browser, was strongly associated with primary forest, whereas its larger congener (red brocket deer) was attracted to secondary growth. We did not find that species predictably fell on a gradient between low-lambda, harvest-sensitive species repulsed by communities and towns, and harvest-tolerant species that may be attracted to communities. Firstly, models were heterogeneous, incorporating both anthropogenic and environmental variables. Secondly, certain small-bodied, high-lambda species including agoutis, acouchis and tinamous, and species typically ignored by hunters such as trumpeters, were also significantly impacted by proximity to communities and urban areas. These species may be behaviourally sensitive to human disturbance and are therefore repelled by human settlements without succumbing to numerical depletion. Agoutis, acouchis and trumpeters were amongst the most frequently detected species by our camera traps and therefore even a weak repulsion signal was likely to be statistically significant. This explanation is, however, inadequate as pacas, which also have a high detection rate, showed no significant depletion effect, despite being highly preferred by hunters.

Grouped detection rate and biomass models paint a clear and consistent picture, suggesting that depletion is indeed occurring, but not in the isotropic, community-centric manner that we anticipated. Any biomass grouping or weighting we created that included hunted species was depressed within the wide neighbourhood to urban areas, whilst the grouped biomass of non-hunted species responded instead to habitat type. This is consistent with the positive correlation in the Médio Juruá region between catch per unit of hunting effort and distance from an urban centre, but not with local human population density (Endo *et al*., 2016). This suggests that depletion is occurring primarily at a landscape rather than local scale.

Another important predictor was distance to a perennial stream. This variable captures a variety of habitat characteristics and many species including tapir are known to prefer areas near water bodies and streams (Bodmer, 1990). Contrary to our expectations, however, overall biomass was significantly lower near streams. This is likely because proximity to perennial streams is also a proxy for accessibility to hunters. Fluvial travel is less laborious than overland travel in tropical forests, especially for hunters transporting heavy carcasses, and perennial streams are therefore important access points into hunting grounds (Peres and Lake, 2003, Chapter 5). This is especially true of both the relatively infrequent long-distance hunts carried out by community members, and the commercial hunting forays carried out by urbanites, both of which are associated with high game-extraction rates (Vega *et al*., 2013, Wilkie *et al*., 2011). The stronger impact of distance to a stream and urban centres than distance to a community, suggests that hunting pressure is anisotropic and urban-centric.

Several of the vertebrate species surveyed here are known to be behaviourally plastic (Oliveira-Santos *et al*., 2010). Nonetheless, though we found that whilst nocturnal detections were relatively more frequent in disturbed areas close to communities, weak species-specific models suggest that we cannot attribute this to species-specific shifts in activity pattern. Instead, this appears to be due to a shift in community composition towards more nocturnal and cathemeral species. This implies that in general, species have a limited capacity to adapt and coexist with human communities and that those species less at risk from human interaction become relatively more common in disturbed areas.

Models of interview data showed that species traits were stronger predictors of distance to first encounters with terrestrial wildlife than were anthropogenic factors. In contrast with other studies (Bodmer *et al*., 1997), the maximum rate of increase was not found to be the most important trait. Instead we found that large-bodied, group-living species were on average detected much farther from communities than small-bodied solitary species. Reported distances suggest that in many communities, the largest-bodied and largest-group-living species were not found even within a day’s return journey from the community.

4.4.2 Alternative explanations for our observations

There are a number of potentially competing explanations for the dual phenomena of lower camera trapping rates in heavily-settled areas and more distant detections of larger-grouped species based on interviews. These species could be changing their behaviour, such that they become less detectable whilst still using areas near communities and urban areas. However, this explanation is implausible because (a) behavioural adaptations are unlikely to influence detection rates at unbaited camera traps placed off trails; (b) our interview respondents, who are longstanding residents, fully familiar with the surroundings of their respective villages, took into account animal signs such as tracks; (c) large-grouped species, such as white-lipped peccary, are almost impossible to overlook, because of their conspicuous bulldozing tracks, if not their noise and scent; and (d) we found weak evidence for species-specific shifts in activity patterns.

Alternatively, these species may be absent from forests in proximity to communities and urban areas due to environmental factors, but this is also implausible. It implies that human communities have chosen parts of the landscape that are relatively inhospitable to large-bodied forest vertebrates, whereas the converse is likely to be the case. Human communities in the Amazon have always chosen the most favourable and productive parts of the landscape (Denevan, 1996). In the absence of human communities, these areas would likely have an elevated population of the large-bodied species relative to the surrounding landscape, because of the higher productivity and consequent food availability, including fruit pulp and seeds. Lastly, these species may have been depleted in proximity to areas of high human population density, repelled from them, or both. The fact that large-bodied, large-grouped species are known to be especially vulnerable to overhunting (Wilkie *et al*., 2011; Ripple *et al*. in press) supports this explanation.

Species that interviewees ranked as frequently hunted were reportedly detected close to communities. This may suggest that the most hunted species are especially resilient and that hunting has little impact on the overall game assemblage. It may even suggest that hunters are deliberately choosing to hunt those species most able to sustain offtake. Alternatively, it may be evidence that hunters have had to switch their prey profile to smaller, more resilient species, having already depleted or repelled the larger species to a distance at which it is no longer profitable to pursue them (Jerozolimski and Peres, 2003). Although our study cannot discriminate between these alternative explanations, our evidence most likely supports the latter, as hunters consistently choose larger-bodied prey such as tapir and white lipped peccaries in landscapes where they are available (Peres and Nascimento, 2006).

4.4.3 Conservative evidence for depletion

We consider the evidence for depletion in this study to be conservative for a number of reasons. Firstly, both of our study regions represent a “best case scenario” in which the proportion of remaining primary forest is high and human population density is low. The large tracts of primary forest beyond easy access likely act as sources, replenishing populations of terrestrial vertebrates in proximity to communities. In both regions, hunting was ranked as a less important livelihood activity and hunted meat was ranked far below fish as an important protein source; we should therefore expect the signal from hunting pressure to be small. In both regions, healthy fisheries provide for the bulk of animal protein requirements (Endo *et al.*, 2016; Amazonas, 2008). In the relatively wealthier Uatumã region, where regular wage labour is more common and market produce is more accessible, subsistence activities in general are less practiced (Börner *et al.*, 2013).

Secondly, our camera trap transects are generally oriented against a primary productivity gradient. Communities and urban areas are typically located in high-productivity portions of the landscape, as commonly observed throughout human pre-history in the Amazon basin (Becher and Meggers, 1973). Transects leading away from communities, along which we deployed cameras, are oriented roughly perpendicular to the main river and the várzea floodplain, and are therefore along a gradient from high productivity floodplains into low productivity upland terra firme forest. This is problematic because soil fertility mediates the density and species richness of nonvolant mammals across Amazonia (Emmons, 1984; Peres, 2008). This bias is unavoidable in our study landscapes. Deploying cameras along transects parallel to the main river would fail to achieve the goal of sampling along a hunting pressure gradient because (a) communities are situated along the river, and therefore a transect leading away from one community would simultaneously approach another; and (b) fluvial access is extremely important to hunters in our study areas, so that all cameras would be equally accessible.

Distance to encounter data from interviews suffers from the same problem as the farther one travels from the community into primary forest, the further one moves away from the fertile floodplain. Moreover, because a high-productivity non-hunted baseline does not exist in our study regions, it is impossible to know what the abundance of different game species would be in the absence of human communities. We may assume therefore that the naturally higher productivity in proximity to communities, partly masks an otherwise stronger depletion effect.

Similarly, it is possible that our snapshot study suffers from a shifted baseline (Milner-Gulland and Bennett, 2003) and that we have failed to fully detect depletion because our study landscapes were already impoverished, under a post-depletion scenario. Though this is certainly a weakness, we doubt that either of our study regions are currently experiencing higher hunting pressure than they experienced historically. In the Uatumã region, Amazonian dark earth (locally, *terra preta)* soils indicate a long history of human habitation (Kern *et al*., 2003), whilst in the Juruá region, the collapse of the rubber industry has likely reduced the reach of hunters compared to half a century ago (Parry *et al*., 2010; Antunes *et al*. 2016).

Thirdly, our camera trap data entirely neglects some of the most harvest-sensitive species, namely the large Ateline primates. Spider and woolly monkeys, which have extremely low reproductive rates compared to similarly-sized terrestrial fauna, have been shown to be some of the first species to become depleted by hunters (Peres, 2000; Peres & Palacios 2007).

Fourthly, our interview data can be heavily biased by detection outliers. Respondents were asked to determine the travel time to a location where one could usually encounter a given species (or its tracks or signs). Nonetheless, several respondents felt that attempting to determine a "typical" encounter location was impossible and instead recalled the closest encounter location from recent memory. An encounter close to the community with a large forest vertebrate such as a tapir is an easily recalled event, but it may not represent a typical encounter distance. Even if tapirs are heavily depleted locally, stochastic environmental and behavioural processes dictate that rare detections close to the community will occur. These outliers thus potentially lead to an underestimation of the extent of faunal depletion based on our interview data.

4.4.4 Appropriate field survey methods

The above concerns thus question which field methods are most appropriate to study faunal depletion in the tropics. Line-transect methods that account only for direct animal encounters, rather than their tracks and signs, are not immune to detectability bias, because hunted species may change their behaviour in hunted areas and become less detectable to surveyors (Fragoso *et al*., 2016). Sign-survey methods have been proposed as a remedy, especially for terrestrial species, because such species are unable to avoid leaving tracks and signs. Sign detectability, however, varies greatly with soil substrate type and recent weather conditions (Munari *et al*., 2011). Camera traps purport to circumvent the aforementioned bias, as species are presumed to be unable to detect and avoid camera traps (but see Séquin, *et al*., 2003 and Gompper, *et al*, 2006), but using photographic rates to infer relative abundance has been criticised for failing to account for detectability differences between both locations and species (Sollmann *et al*., 2013).

All of the aforementioned methods are spatially and temporally limited. High financial cost and the potential to disrupt the livelihoods of community members, prohibit their intensive and long-term use in proximity to communities. Interviews avoid this problem by drawing on the long-term cognitive experience accumulated by community members with extensive knowledge of their forest environments. For instance, our camera trap dataset represents only 32.9 years of detection effort, whereas our interview data draws on roughly four times more experience. This is especially advantageous for species such as white lipped peccary, which require extensive survey effort to accumulate sufficient independent detections on which to base meaningful inferences because of their extremely low herd densities and extremely large home range size. Interviews can also reduce detection biases associated with line-transect censuses as experienced hunters can quantify track and sign density. However, interview data can suffer from retrospective bias (O'Donnell *et al*., 2010), social desirability bias (Nuno and John, 2015), and the influence of outliers as discussed above. We therefore argue that no single technique is free from error and bias and that interview data makes a valuable contribution to understanding faunal depletion.

4.4.5 Evidence for density compensation in peccaries

Our camera trap and interview data suggest that in the Uatumã region, the biomass of competitively released collared peccaries compensates for the absence of white lipped peccaries. In both regions, peccaries represent the highest detected biomass of any terrestrial vertebrate. In the Uatumã region, populations of white lipped peccaries are currently either very low or occupying areas far from communities. Collared peccaries by contrast were detected at rate three times higher (camera trap data) and at distances on average five kilometres closer (interview data) to communities in the Uatumã region than in the Juruá. Being larger bodied, travelling in far larger groups and exploiting many of the same food-sources, white lipped peccaries are thought to outcompete and thereby depress the population of collared peccaries.

4.4.6 Study limitations and future directions

Our study design could have been strengthened in a number of ways. We lacked additional camera trap sampling effort in areas of very high hunting pressure. We believe that in our study landscapes, where hunting is infrequent, a strong depletion signal is only apparent relatively close to communities. Had time permitted, we would therefore have sampled the peri-community agricultural mosaics in the Uatumã region, and devoted more sampling effort to areas near towns in both landscapes. This strategy has drawbacks, however, in that areas close to communities are more deforested, thereby adding a challenge in disentangling these effects. One could sample primary forest remnants in proximity to communities to partly mitigate this. Another fruitful approach would be to sample multiple landscapes, in which the availability of aquatic protein resources, and therefore the necessity to hunt, varies greatly. In order to avoid the confounding effects of productivity gradients, one would need to sample highly productive, but unhunted areas in tandem with adjacent hunted areas (Arcese and Sinclair, 1997). Such experimentally ideal landscapes are rare or non-existent, however, partly due to the high opportunity cost of setting them aside as strictly protected areas. Alternatively, one could conduct longitudinal studies (Hill *et al*., 2003), ideally by either investigating areas before and after colonisation, or during the process of abandonment. Such studies, although valuable, are again rare due to the difficulty of establishing and maintaining a long-term research presence in rural tropical areas. Although we investigated faunal depletion, it was beyond the scope of this study to investigate the sustainability of subsistence hunting in these regions. To do so would require both long-term and detailed hunting offtake data in tandem with species abundance data.

4.5 Conclusions

In lowland Amazonia, conditions favourable to the persistence of game vertebrates, including modest human population densities, alternative sources of animal protein in the form of abundant fish stocks (McGrath *et al*., 1993; Rushton *et al*. 2005), and large areas of primary forest refugia are not uncommon (Fa and Peres, 2002). Indeed, human population density in the Amazon basin is lower than in any other tropical biodiversity hotspot or wilderness area (Cincotta *et al*., 2000). As such, the persistence of large game vertebrates in our study regions may be broadly representative of other central Amazonian sites. This does not justify complacency however. In other tropical forest regions where human population densities and game extraction rates are far higher, game depletion is likely far more severe. Moreover, human population growth rates in tropical biodiversity hotspots and wilderness areas generally exceed the average population growth rate worldwide (Cincotta *et al*., 2000). Tropical forest management strategies, which have often proved challenging (García-Fernández *et al*., 2008), may become increasingly important in human-occupied protected areas.

Despite a widely replicated study design including both camera traps and interviews, our evidence for anthropogenic depletion of terrestrial forest vertebrates is mixed. We conclude that in our “best case scenario” regions, which simultaneously retain a high proportion of primary forest cover and a low human population density with access to alternative protein, only a select few species have been depleted in proximity to communities. We found limited evidence that individual species shift their activity patterns in response to human settlements. Instead, species composition is anthropogenically disturbed areas is apparently comprised of a larger fraction of nocturnal species. Interview data suggest that depletion is strongly predicated on species traits, with large-bodied large-group-living species the worst impacted. Urban areas cause landscape-scale reduction in the overall biomass of the terrestrial vertebrate assemblage. We cannot know how intact the overall faunal assemblage is relative to a high-productivity, un-hunted baseline, because none exists. Strictly protected areas offer invaluable insights in this respect. We cannot further elucidate the degree to which sustainable-use protected areas effectively safeguard intact faunal assemblages, because protected status was confounded by distance to urban areas. Nonetheless, our sparsely inhabited study regions clearly retain the entire spectrum of the terrestrial vertebrate fauna, suggesting that as it stands, sustainable-use tropical forest reserves are not incompatible with biodiversity conservation.

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APPENDICES

APPENDIX A - Methodological Notes

1. For camera trap deployments, Bushnell Trophy-Cam, Trophy-Cam HD, and Reconyx HC500 Hyperfire models were used. Camera sensors were set to high sensitivity. They took 3 sequential burst photographs or 3 second video clips. A red light flash was used in very low light. We attempted to deploy all cameras for 30 days, but malfunction, theft (or the threat of theft) and other logistical difficulties meant that deployment period varied somewhat. Deployments were not made in *várzea*. In order to control for the bias introduced by species-specific responses to trails, deployments along transects in primary forest were always deployed ~20m away from trails and facing away from the trail where possible. These transects used Probuc faunal monitoring trails where available. Where these were unavailable, suitable locations were identified in GIS to avoid impassable rivers and swamps and temporary trails were cut by ourselves. In areas where unforeseen obstacles such as swamps made deployment at the designated distance along the transect impossible, or if it was judged to be too late in the day to reach 6km and return before nightfall, cameras were deployed in the closest available location. Deployments outside contiguous primary forest were 25m from the habitat edge to control for edge effects. When deploying cameras in proximity to local communities, a community resident was employed to aid in the identification of suitable locations and determine the age of capoeiras since abandonment. Locations were not chosen to deliberately maximise detection (for example beneath fruiting trees), but conspicuous obstacles to detection were avoided. Bait was not used. Locations were chosen to have relatively flat ground, relatively unobscured by large trees/obstacles. Thin vegetation was cleared in a cone of 7 paces long by 7 paces wide in-front of the camera to permit detection and avoid detecting the movement of vegetation. Cameras were deployed at knee height, attached to trees. Walk-tests were performed to confirm correct positioning. Mothballs and tampons were put inside cameras along with batteries to repel insects and protect against humidity. A GPS waypoint was always taken. When cameras were removed, a note was made of any problems or malfunctions such as water ingress, insect attack, dislodgement or battery failure.
2. When summarising interview data, where single numeric responses were given, means were calculated. Where multiple unranked categorical responses were given, the number of responses per category were summed. Where multiple ranked categorical responses were given, a summed, rank-weighted score per category was calculated ($\sum (\sum (\text{ranked1}) + \sum (\text{ranked2}/2) + \sum (\text{ranked3}/3) \ldots)$).

3. To calculate transport distance we used average speeds per transport type from Parry and Peres, 2015. Outboard motor (locally *rabeta*) 9km/h, un-motorised canoe 5km/h, on foot 4km/h. These mean speeds are confirmed by our fieldwork experience.

APPENDIX B – Species activity patterns

The table below displays how camera trap detection data per species were converted into an activity pattern designation. The first photograph of every independent detection per species was assigned a temporal period as follows (1) day – between 07:00 and 17:00 (2) night - between 19:00 and 05:00 (3) dawn/dusk - between 05:00 and 07:00 and between 17:00 and 19:00. For each species the proportion of detections in each category were calculated. Species with a daytime detection proportion < 0.15 were designated nocturnal. Species with a night-time detection proportion < 0.15 were designated diurnal. All other species were designated cathemeral.

Species	Dawn.dusk proportion	Day proportion	Night proportion	designation
Leopardus pardalis	0.20	0.21	0.60	cathemeral
Leopardus wiedii	0.13	0.20	0.67	cathemeral
Mazama americana	0.22	0.29	0.49	cathemeral
Mazama nemorivaga	0.20	0.65	0.15	cathemeral
Panthera onca	0.20	0.60	0.20	cathemeral
Puma concolor	0.21	0.45	0.33	cathemeral
Tayassu pecari	0.20	0.60	0.20	cathemeral
Atelocynus microtis	0.18	0.79	0.03	diurnal
Crypyurellus spp	0.42	0.58	0.00	diurnal
Dasyprocta fuliginosa	0.30	0.70	0.01	diurnal
Eira barbara	0.13	0.85	0.02	diurnal
Leptotila spp	0.13	0.87	0.00	diurnal
Mitu tuberosum	0.21	0.79	0.00	diurnal
Myoprocta pratti	0.62	0.37	0.01	diurnal
Myrmecophaga tridactyla	0.23	0.68	0.09	diurnal
Nasua nasua	0.22	0.78	0.00	diurnal
Odontophorus spp	0.25	0.75	0.00	diurnal
Ortalis guttata	0.00	1.00	0.00	diurnal
Pecari tajacu	0.10	0.87	0.04	diurnal
Penelope jacquacu	0.12	0.88	0.00	diurnal
Psophia leucoptera	0.14	0.86	0.00	diurnal
Puma yagouaroundi	0.25	0.75	0.00	diurnal
Sciurus iginitus	0.00	1.00	0.00	diurnal
Sciurus spadiceus	0.03	0.97	0.00	diurnal
Tinamus spp	0.40	0.60	0.00	diurnal
Cuniculus paca	0.05	0.00	0.95	nocturnal
Dasyspus spp	0.03	0.00	0.97	nocturnal
Didelphis marsupialis	0.12	0.00	0.88	nocturnal
Echimyidae spp	0.17	0.00	0.83	nocturnal
Metachirus spp	0.14	0.00	0.86	nocturnal
Nonspecific Cingulata small	0.03	0.00	0.97	nocturnal
Priodontes maximus	0.23	0.00	0.77	nocturnal
Procyon cancrivorus	0.00	0.00	1.00	nocturnal
Tamandua tetradactyla	0.11	0.11	0.78	nocturnal
Tapirus terrestris	0.22	0.05	0.73	nocturnal

APPENDIX C - Species relatedness

When creating multivariate models that include species traits, it was important to account for both multiple measurements of the same species and for species relatedness. The table below displays the taxonomic classification of each study species. A relatedness matrix (see below) was created in order to visually assess the taxonomic "distance" between species. A taxonomic distance was designated in which species in the same genus, family, order or class were designated 2, 3, 4 or 5 respectively. Species not in the same class were designated 6. Ideally, species traits models would include the main taxonomic levels as nested random effects as per Dulvy *et al*., 2014. Our study species are however spread amongst three classes and include few congeners. Therefore we included "family" and "species" as nested random effects.

Species	Genus	Family	Order	Class
Leptotila spp	Leptotila	Columbidae	Columbiformes	Aves
Mitu Crax spp	Mitu/Crax	Cracidae	Galliformes	Aves
Ortalis guttata	Ortalis	Cracidae	Galliformes	Aves
Penelope jacquacu	Penelope	Cracidae	Galliformes	Aves
Odontophorus spp	Odontophorus	Odontophoridae	Galliformes	Aves
Psophia spp	Psophia	Psophiidae	Gruiformes	Aves
Crypturellus spp	Crypyurellus	Tinamidae	Tinamiformes	Aves
Tinamus spp	Tinamus	Tinamidae	Tinamiformes	Aves
Mazama americana	Mazama	Cervidae	Artiodactyla	Mammalia
Mazama nemorivaga	Mazama	Cervidae	Artiodactyla	Mammalia
Pecari tajacu	Pecari	Tayassuidae	Artiodactyla	Mammalia
Tayassu pecari	Tayassu	Tayassuidae	Artiodactyla	Mammalia
Atelocynus microtis	Atelocynus	Canidae	Carnivora	Mammalia
Leopardus pardalis	Leopardus	Felidae	Carnivora	Mammalia
Leopardus wiedii	Leopardus	Felidae	Carnivora	Mammalia
Panthera onca	Panthera	Felidae	Carnivora	Mammalia
Puma concolor	Puma	Felidae	Carnivora	Mammalia
Puma yagouaroundi	Puma	Felidae	Carnivora	Mammalia
Eira barbara	Eira	Mustelidae	Carnivora	Mammalia
Nasua nasua	Nasua	Procyonidae	Carnivora	Mammalia
Procyon cancrivorus	Procyon	Procyonidae	Carnivora	Mammalia
Priodontes maximus	Priodontes	Chlamyphoridae	Cingulata	Mammalia
Nonspecific Cingulata small	Unspecified.2	Unspecified.3	Cingulata	Mammalia
Didelphis marsupialis	Didelphis	Didelphidae	Didelphimorphia	Mammalia
Metachirus spp	Metachirus	Didelphidae	Didelphimorphia	Mammalia
Tapirus terrestris	Tapirus	Tapiridae	Perissodactyla	Mammalia
Myrmecophaga tridactyla	Myrmecophaga	Myrmecophagidae	Pilosa	Mammalia
Tamandua tetradactyla	Tamandua	Myrmecophagidae	Pilosa	Mammalia
Alouatta spp	Alouatta	Atelidae	Primates	Mammalia
Ateles spp	Ateles	Atelidae	Primates	Mammalia
Lagothrix spp	Lagothrix	Atelidae	Primates	Mammalia
Cuniculus paca	Cuniculus	Cuniculidae	Rodentia	Mammalia
Dasyprocta spp	Dasyprocta	Dasyproctidae	Rodentia	Mammalia
Myoprocta spp	Myoprocta	Dasyproctidae	Rodentia	Mammalia
Echimyidae spp	Unspecified.1	Echimyidae	Rodentia	Mammalia
Sciurus ignitus	Sciurus	Sciuridae	Rodentia	Mammalia
Sciurus spadiceus	Sciurus	Sciuridae	Rodentia	Mammalia
Chelonoidis spp	Chelonoidis	Testudinidae	Testudines	Sauropsida

	Leptotila spp	Mitu Crax spp	Ortalis guttata	Penelope jacquacu	Odontophorus spp	Psophia spp	Crypyurelus spp	Tinamus spp	Mazama americana	Mazama nemorivaga	Pecari tajacu	Tayassu pecari	Atelocynus microtis	Leopardus pardalis	Leopardus wiedii	Panthera onca	Puma concolor	Puma yagouaroundi	Eira barbara	Nasua nasua	Procyon cancrivorus	Priodontes maximus	Nonspecific Cingulata sm	Didelphis marsupialis	Metachirus spp	Tapirus terrestris	Myrmecophaga tridactyla	Tamandua tetradactyla	Alouatta spp	Ateles spp	Lagothrix spp	Cuniculus paca	Dasyprocta spp	Myoprocta spp	Echimyidae spp	Sciurus ignitus	Sciurus spadiceus	Chelonoidis spp
Leptotila spp	1	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Mitu Crax spp	5	1	3	3	4	5	5	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Ortalis guttata	5	3	1	3	4	5	5	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Penelope jacquacu	5	3	3	1	4	5	5	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Odontophorus spp	5	4	4	4	1	5	5	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Psophia spp	5	5	5	5	5	1	5	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Crypyurelus spp	5	5	5	5	5	5	1	3	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Tinamus spp	5	5	5	5	5	5	3	1	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Mazama americana	6	6	6	6	6	6	6	6	1	2	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Mazama nemorivaga	6	6	6	6	6	6	6	6	2	1	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Pecari tajacu	6	6	6	6	6	6	6	6	4	4	1	3	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Tayassu pecari	6	6	6	6	6	6	6	6	4	4	3	1	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Atelocynus microtis	6	6	6	6	6	6	6	6	5	5	5	5	1	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Leopardus pardalis	6	6	6	6	6	6	6	6	5	5	5	5	4	1	2	3	3	3	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Leopardus wiedii	6	6	6	6	6	6	6	6	5	5	5	5	4	2	1	3	3	3	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Panthera onca	6	6	6	6	6	6	6	6	5	5	5	5	4	3	3	1	3	3	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Puma concolor	6	6	6	6	6	6	6	6	5	5	5	5	4	3	3	3	1	2	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Puma yagouaroundi	6	6	6	6	6	6	6	6	5	5	5	5	4	3	3	3	2	1	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Eira barbara	6	6	6	6	6	6	6	6	5	5	5	5	4	4	4	4	4	4	1	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Nasua nasua	6	6	6	6	6	6	6	6	5	5	5	5	4	4	4	4	4	4	4	1	3	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Procyon cancrivorus	6	6	6	6	6	6	6	6	5	5	5	5	4	4	4	4	4	4	4	3	1	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Priodontes maximus	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	1	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Nonspecific Cingulata sma	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	4	1	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
Didelphis marsupialis	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	1	3	5	5	5	5	5	5	5	5	5	5	5	5	6
Metachirus spp	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	3	1	5	5	5	5	5	5	5	5	5	5	5	5	6
Tapirus terrestris	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	1	5	5	5	5	5	5	5	5	5	5	5	6
Myrmecophaga tridactyla	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	1	3	5	5	5	5	5	5	5	5	5	6
Tamandua tetradactyla	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	3	1	5	5	5	5	5	5	5	5	5	6
Alouatta spp	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	1	3	3	5	5	5	5	5	5	6
Ateles spp	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	3	1	3	5	5	5	5	5	5	6
Lagothrix spp	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	3	3	1	5	5	5	5	5	5	6
Cuniculus paca	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	1	4	4	4	4	4	6
Dasyprocta spp	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	1	3	4	4	4	6
Myoprocta spp	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	3	1	4	4	4	6
Echimyidae spp	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	4	4	1	4	4	6
Sciurus ignitus	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	4	4	4	1	2	6
Sciurus spadiceus	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	4	4	4	2	1	6
Chelonoidis spp	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	1

APPENDIX D – Grouped biomass GLMMs

The table below displays the explanatory variables retained in GLMMs of detected group biomass, along with coefficients, adjusted standard errors and P values.

Sp.code	Var.code	Coefficient	Adj.stder	P.value
All	TOWN	-0.28228	0.08346	<0.001
All	COM.DIST	-0.04657	0.08634	>0.05
All	COM.POP	-0.063	0.09321	>0.05
All	ELEV	-0.04628	0.08481	>0.05
All	PRIMARY	0.13324	0.08126	>0.05
All	STREAM	0.16131	0.07829	<0.05
All.nq	TOWN	-0.27241	0.06632	<0.001
All.nq	COM.DIST	0.09012	0.06992	>0.05
All.nq	ELEV	0.0291	0.06912	>0.05
All.nq	PRIMARY	0.07321	0.07417	>0.05
All.nq	STREAM	0.15184	0.06651	<0.05
Bin.hunt	TOWN	-0.39891	0.09828	<0.001
Bin.hunt	COM.POP	-0.06411	0.10778	>0.05
Bin.hunt	PRIMARY	0.11254	0.09086	>0.05
Bin.hunt	STREAM	0.1959	0.08755	<0.05
Bin.hunt.nq	TOWN	-0.38499	0.08101	<0.001
Bin.hunt.nq	COM.DIST	0.10934	0.08043	>0.05
Bin.hunt.nq	ELEV	0.03639	0.08157	>0.05
Bin.hunt.nq	PRIMARY	0.06741	0.0818	>0.05
Bin.hunt.nq	STREAM	0.18885	0.07518	<0.05
Bin.huntpers	TOWN	-0.34798	0.09343	<0.001
Bin.huntpers	COM.POP	-0.06461	0.09867	>0.05
Bin.huntpers	ELEV	-0.02542	0.09203	>0.05
Bin.huntpers	PRIMARY	0.12514	0.08996	>0.05
Bin.huntpers	STREAM	0.17802	0.0846	<0.05
Bin.huntpers.nq	TOWN	-0.34023	0.07644	<0.001
Bin.huntpers.nq	COM.DIST	0.0937	0.07755	>0.05
Bin.huntpers.nq	PRIMARY	0.05955	0.07964	>0.05
Bin.huntpers.nq	STREAM	0.16717	0.07289	<0.05
Bin.pers	COM.DIST	-0.1003	0.1994	>0.05
Bin.pers	ELEV	-0.1592	0.1703	>0.05
Bin.pers	STREAM	-0.0792	0.2182	>0.05
Bin.unpers	TOWN	0.1657	0.1323	>0.05
Bin.unpers	COM.DIST	0.1192	0.1552	>0.05
Bin.unpers	PRIMARY	0.3169	0.1413	<0.05
Bin.unpers	STREAM	0.1194	0.1506	>0.05
Hw	TOWN	-0.42262	0.10857	<0.001
Hw	COM.DIST	-0.03526	0.1008	>0.05
Hw	COM.POP	-0.08402	0.12036	>0.05
Hw	PRIMARY	0.13238	0.09871	>0.05
Hw	STREAM	0.18371	0.09272	<0.05
Hw.nq	TOWN	-0.42189	0.08414	<0.001
Hw.nq	COM.DIST	0.0853	0.08382	>0.05
Hw.nq	ELEV	0.04413	0.08576	>0.05
Hw.nq	PRIMARY	0.05169	0.08481	>0.05
Hw.nq	STREAM	0.1769	0.07755	<0.05
Rw	TOWN	-0.35806	0.08113	<0.001
Rw	COM.DIST	0.02467	0.08153	>0.05
Rw	STREAM	0.12498	0.07362	>0.05
Rw.nq	TOWN	-0.35491	0.08127	<0.001
Rw.nq	COM.DIST	0.0324	0.08147	>0.05
Rw.nq	STREAM	0.125	0.0734	>0.05

APPENDIX E – Species activity pattern GLMMs

The table below displays the explanatory variables retained in GLMMs of activity patterns per species, along with coefficients, adjusted standard errors and P values.

Sp.code	Var.code	Coefficient	Adj.Stder	P.value
All	TOWN	0.04978	0.03739	>0.05
All	COM.DIST	-0.07947	0.03694	<0.05
All	ELEV	-0.03786	0.03711	>0.05
All	PRIMARY	-0.11411	0.03298	<0.001
All	STREAM	-0.0577	0.03591	>0.05
Atel.mi	COM.POP	0.5305	0.3406	>0.05
Cryp.sp	COM.POP	-2.0551	2.4214	>0.05
Dasy.sp	TOWN	0.07292	0.1889	>0.05
Dasy.sp	COM.DIST	-0.09429	0.12332	>0.05
Dasy.sp	ELEV	0.06982	0.12264	>0.05
Dasy.sp	PRIMARY	0.04156	0.11959	>0.05
Dasy.sp	STREAM	-0.23526	0.13431	>0.05
Eira.ba	COM.DIST	-0.9346	0.8579	>0.05
Eira.ba	PRIMARY	-0.4271	0.3841	>0.05
Leop.pa	COM.DIST	-0.11857	0.1889	>0.05
Leop.pa	COM.POP	0.12805	0.15238	>0.05
Leop.pa	PRIMARY	-0.06726	0.09424	>0.05
Maza.am	COM.DIST	-0.1764	0.11709	>0.05
Maza.am	COM.POP	-0.11329	0.11997	>0.05
Maza.am	ELEV	0.06759	0.07381	>0.05
Maza.am	PRIMARY	-0.08832	0.06186	>0.05
Maza.am	STREAM	0.15869	0.09832	>0.05
Maza.ne	TOWN	-0.10492	0.14008	>0.05
Maza.ne	COM.DIST	-0.3832	0.14846	<0.01
Maza.ne	COM.POP	0.13039	0.09974	>0.05
Maza.ne	ELEV	0.09613	0.10842	>0.05
Maza.ne	PRIMARY	0.18358	0.26184	>0.05
Maza.ne	STREAM	-0.20929	0.14915	>0.05
Mitu.Cr	COM.DIST	-0.1339	0.3009	>0.05
Mitu.Cr	COM.POP	0.239	0.2342	>0.05
Mitu.Cr	ELEV	-0.2313	0.3105	>0.05
Mitu.Cr	PRIMARY	-0.4186	0.312	>0.05
Mitu.Cr	STREAM	0.4964	0.2677	>0.05
Myop.sp	TOWN	-0.17719	0.16753	>0.05
Myop.sp	COM.DIST	0.08608	0.11055	>0.05
Myop.sp	COM.POP	-0.1447	0.24524	>0.05
Myop.sp	PRIMARY	-0.24435	0.28806	>0.05
Myrm.tr	ELEV	-0.4863	0.4381	>0.05
Nasu.na	ELEV	-4.2551	4.6063	>0.05
Nasu.na	STREAM	0.8242	2.6754	>0.05
Pant.on	TOWN	0.6514	0.3779	>0.05
Pant.on	PRIMARY	-0.5894	0.4239	>0.05
Peca.ta	TOWN	0.5274	0.3573	>0.05
Peca.ta	ELEV	0.5241	0.2654	<0.05
Peca.ta	PRIMARY	-0.7368	0.3176	<0.05
Peca.ta	STREAM	0.3858	0.313	>0.05
Psop.sp	TOWN	-0.0289	0.37628	>0.05
Psop.sp	COM.DIST	-0.03811	0.3533	>0.05
Psop.sp	COM.POP	-1.28468	1.08378	>0.05
Psop.sp	ELEV	-0.15088	0.33271	>0.05
Psop.sp	PRIMARY	-0.59281	0.60047	>0.05
Psop.sp	STREAM	0.32448	0.2847	>0.05
Sciu.sp	COM.POP	-1.418	205.266	>0.05
Sciu.sp	ELEV	-2.815	157.325	>0.05
Tina.sp	STREAM	-0.7874	0.7686	>0.05

Chapter 5: Trialling novel GPS units to characterise simulated hunts with domestic dogs in Brazilian Amazonia

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Abstract

The use of domestic dogs as a hunting technology is controversial and understudied in the humid tropics. Hunting dogs are believed to exacerbate the depletion and/or repulsion of terrestrial game fauna, and to spread diseases to wild canids. Nonetheless, diverse semi-subsistence agriculturalist and hunter-gatherer peoples attest to the usefulness of hunting dogs in augmenting game yields and defending against damaging crop raiders. Studying the spatial behaviour of hunting dogs has proven challenging both because of social stigma and inadequate technology. In this study we trialled novel, lightweight and open source Mataki GPS units in tandem with three types of commercially available GPS units during 30 simulated hunts in the Juruá and Uatumã regions of central-western Brazilian Amazonia. We found that, despite the fact that domestic dogs were commonly used to protect agricultural plots, several respondents expressed concerns that hunting dogs are detrimental to populations of game fauna. On average, participants in simulated hunts spent the largest proportion of their time in primary upland and lowland forest and relatively little time in areas of nonforest or secondary growth (78.3 ± 3.6% and 11.4 ± 2.2% respectively). Simulated hunts that began in towns involved more bred hunting dogs and covered significantly longer distances than did those which began outside towns. Simulated hunts in the Juruá region involved more people, guns, dogs and bred hunting dogs than in the Uatumã region. Whilst these results could be taken as evidence of both hunting-mediated depletion in proximity to cities and of region-specific hunting cultures, we treat these conclusions with caution due to the biases inherent in our study. Though dogs covered ~ 13% more ground than humans during simulated hunts, the difference was not as pronounced as initially anticipated. All of the dogs surveyed remained close to their human masters, and spent over 60% of their time <11m from human tracks. Specially bred hunting dogs did however venture significantly further than non-specialist dogs. The social and ecological costs and benefits of hunting dogs in the tropics requires far more in-depth study in order to inform conservation policy and management.

5.1 Introduction

The initial divergence of *Canis lupus familiaris* from *Canis lupus* >100,000 years ago (Vilà*et al*., 1997), predates even domesticated cereals by an order of magnitude (Colledge and Conolly, 2007). They are now the world's most widespread and abundant carnivore due to introduction and domestication by humans (Wandeler *et al*., 1993). As hunting companions they have been and continue to be used by diverse groups (Clutton-Brock and Noe-Nygaard, 1990), for subsistence (Terashima, H., 1983 - Mbuti in DR Congo; Brosius, 1991 – Penan in Borneo), commercial (Fa and Yuste, 2001 - Equatorial Guinea), and sport hunting (Luskin *et al*., 2014 Minangkabau in Sumatra). Domestic hunting dogs have been shown to be a potent tool, substantially increasing the efficiency of hunts, and several prey species, including nine banded armadillo (*Dasypus novemcintus*), are virtually impossible to capture without the aid of dogs (De Souza-Mazurek *et al*., 2000; Alves *et al*., 2009).

Hunting dogs have also been implicated in the unsustainable depletion and spatial disruption of terrestrial fauna. They are a favoured tool of illegal poachers (Gandiwa, 2011) and are believed to have a drastic impact (Galetti and Sazima, 2006); covering long distances, killing small game, maiming and chasing away larger animals and causing additional disturbance through their noise and scent (Gompper, 2013). Furthermore, domestic, semi-feral, and feral dogs (whether used during hunts or not) host diseases including canine distemper and rabies, which infect populations of wild carnivores (Alexander and Appel, 1994; Butler *et al*., 2004). These deleterious effects compound the widely documented depletion of tropical forest game fauna, both in the Amazon (Peres, 2000) and globally (Redford, 1992; Ripple *et al*. in press). As a result, there have been calls to enforce bans on the use of dogs as a hunting tool in Brazil (Carvalho and Pezzuti, 2010) and elsewhere (Coad, 2008).

Domestic dogs (hereafter, dogs) are nonetheless an important livelihood tool for semi-subsistence communities. In addition to their role in increasing the efficiency of protein acquisition, they are used as guard dogs to protect people and livestock against large felids (Gonzalez, *et al*., 2012), although dogs have themselves been implicated in livestock predation (Verdade and Campos, 2004) and numerous attacks on humans (http://www.who.int/mediacentre/factsheets/fs373/en/). Moreover, semi-subsistence agriculturalists attest that they confer valuable protection against terrestrial vertebrate crop raiders. In our study (Chapter 3) in the Juruá region, amongst the strategies to suppress crop raiding, 17.1% of responses involved hunting with dogs, or using dogs to scare away crop raiders.

Despite the high social benefits and ecological costs of using hunting dogs, research into their behaviour, especially during hunts is scarce and generally confined to temperate regions (Claridge *et al*., 2009; Shubkina *et al*., 2010). The literature surrounding domestic dogs and biodiversity conservation in the tropics tends to either focus on the effects of free-ranging semi-feral dogs

(Woodroffe and Donnelly, 2011; Gompper, 2013) or the use of dogs as tools by subsistence hunters (Koster, 2009). Less attention has been paid to characterising the spatial behaviour of domestic dogs during hunts, though the behavioural ecology of related canids such as African wild dogs during hunts in Africa (Creel and Creel, 2002) and dingoes in Australia has been studied (Claridge, 2009). Conservationists are therefore armed with scant evidence with which to determine the level of threat that hunting dogs pose. Denouncing the use of hunting dogs based on such evidence, despite their clear usefulness to semi-subsistence communities, could fuel resentment from the very people whose local support conservationists so desperately need.

Social stigma and technological limitations have hampered efforts to study the behaviour of hunting dogs in the tropics. The consumption of wild-caught meat is only legal in Brazil for rural subsistence and the use of hunting dogs is illegal (Cunha and Almeida, 2000; Parry *et al*, 2014). In Brazilian Amazonia, many communities are simultaneously afraid of falling afoul of governmental environmental protection agencies, and wary of the intervention of wealthy, conservation-oriented outsiders in their livelihoods. Illegal activities such as commercial fishing within protected lakes, can result in a denouncement and the intervention of the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA), who can confiscate equipment and issue fines (McGrath, *et al*., 2004; Parry *et al*., 2014). Rural communities are often poorly informed about wildlife legislation (Keane *et al*., 2011) and in our study regions, the legal status of hunting in general and the use of dogs in particular is not well understood. In addition, conservation NGOs have been keen to disseminate environmental awareness, and discourage activities they consider to be unsustainable. These factors create a climate, in which hunting with dogs is perceived to be both risky and socially vilified. This poses a considerable barrier to researchers attempting to gain an accurate and unbiased insights into this potential human-wildlife conflict.

Additionally, GPS receivers and other tracking devices have historically been too bulky, expensive and/or inaccurate under dense canopy cover to deploy with sufficient replication to characterise the movement patterns of hunting dogs in tropical forests. Within the past decades, however, rapid improvements and cost reduction in GPS, radio-telemetry and geo-locator technology have resulted in considerable advances in the field of animal movement ecology (Bridge *et al*., 2011). The accuracy, bulk and cost of GPS units have been simultaneously reduced. A variety of low cost GPS options are now being used and tested by research teams in diverse fields (Duncan *et al*., 2013). The Mataki Technology for Nature initiative (http://www.technologyfornature.org/project/tracking-behaviour-in-the-wild/) typifies this trend. This partnership between the Zoological Society of London, University College London and Microsoft Research, explicitly aims to provide conservation researchers and practitioners with low cost, high quality and open source technology. In the midst of chronic biodiversity conservation underfunding (Waldron *et al*., 2013), it is a welcome development.

In this study, we intend to (1) compare the accuracy, reliability and overall usability of Mataki GPS devices, with commercially available alternatives; (2) broadly characterise a series of simulated hunts across our two study regions; (3) determine the degree to which dogs cause additional disturbance to humans insofar as they travel farther than, and cover an area distinct to their masters; and (4) assess the prevalence of dogs as a hunting tool and record the attitudes of local community members towards hunting dogs using interviews.

5.2 Methods

5.2.1 Study region

This study was carried out in the Médio Juruá and Uatumã regions of Western and Central Brazilian Amazonia (Fig. 5.1). The Médio Juruá study region covers an area of 1,637,008 ha and consists of 63.9% of primary unflooded (*terra firme*) forest, 30.0% of seasonally-flooded *várzea* forest, 4.4% of permanent water bodies, which include the Juruá River (the second-largest white-water tributary of the Amazon) and its tributaries and oxbow lakes, and 1.8% deforestation. Two sustainable-use reserve -- the Uacari Sustainable Development Reserve and the Médio Juruá Extractive Reserve -- jointly legally protect 42.3% of this landscape. The nearest towns are Carauari, which is 88 fluvial km downstream from the Médio Juruá Reserve and has a population of 4145 families, and Itamarati, which is 120 fluvial km upstream from the Uacari Reserve and has a population of 905 families.

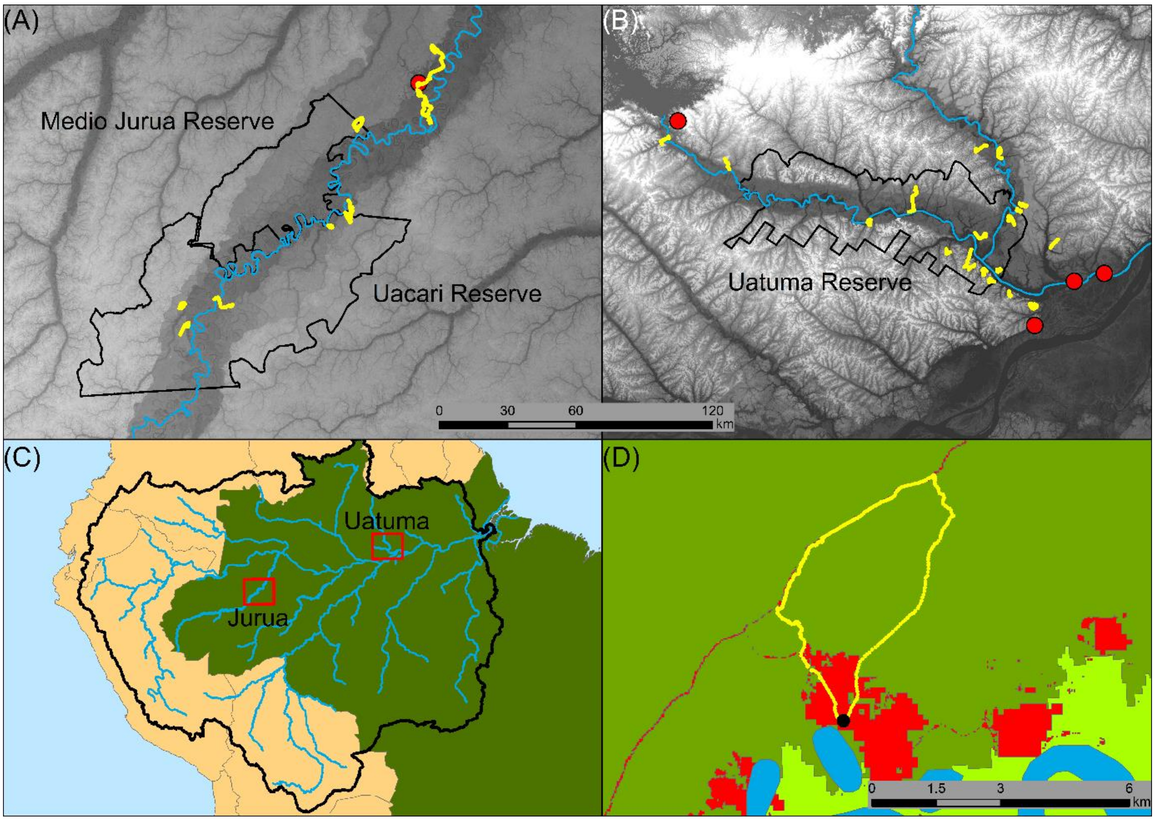

***Figure 5.1**: Geographic location of the Juruá (A) and Uatumã (B) study regions within the Brazilian Amazon (C), and an example simulated hunt (D). Panels A and B, which are presented at the same scale, show a digital elevation (SRTM) map, with darker shades indicating lower elevation. Rivers, towns and survey tracks are represented as blue lines, red circles and yellow lines, respectively, whilst reserve boundaries are outlined in black. The Amazon basin (C) is outlined in black and the Juruá and Uatumã study regions are indicated by red boxes. In panel D, the background is a landcover classification with primary upland forest, primary floodplain forest, permanent water bodies and deforestation in dark green, light green, blue and red respectively. The centre of a local community is indicated by a solid circle, whilst the survey track is indicated in yellow.*

The Uatumã study region covers an area of 1,601,704 ha and consists of 62.3% of undulating upland primary unflooded (*terra firme*) forest, 17.9% of primary low-lying and seasonally-flooded *igapo* forest, 11.1% permanent water bodies, which include the Uatumã River (which connects the Balbina reservoir to the Solimões River) and its main tributary the Jatapú River, 4.0% deforestation and 4.7% of campina and campinarana non-forest vegetation on oligotrophic soils. The Uatumã Sustainable Development Reserve legally protects 27.0% of this landscape. The nearest towns are Vila Balbina, which has a population of 420 families and is 66 fluvial km upstream of the reserve, and Sao Sebastião, Itapiranga and Urucará, with populations of 1214, 1345 and 2051 families, respectively, and are 37, 40, and 53 fluvial km downstream of the reserve, respectively.

Both regions are inhabited by *ribeirinhos* who are former rubber-tapper semi-subsistence communities of mixed-descent, with producer cooperatives and resource-management programs. Large-scale ecological and socioeconomic differences between the two study regions are due to river chemistry and proximity to Manaus, the largest city in the state of Amazonas. The Juruá region encompasses highly productive white-water floodplain ecosystems, whereas the Uatumã region encompasses less productive black-water ecosystems, potentially resulting in lower faunal biomass density at Uatumã. Secondly, the Juruá region is over five times farther from Manaus, which increases transaction costs and reduces market opportunities for Juruá inhabitants.

5.2.2 GPS deployment

During this study, Garmin 60Csx and Garmin Etrex10 devices (Garmin Ltd., USA), Igotu GT120 devices (Mobile Action Technology Inc., Taiwan), and novel Mataki open-source GPS devices were used (Mataki.org; 2013). The latter were provided free of charge, by the Mataki, Technology for Nature collaboration. GPS devices were deployed during three phases/scenarios a) UK Mataki tests - These were conducted in the UK prior to Brazilian fieldwork, in order to determine the feasibility of using novel Mataki devices and to determine the correct data capture settings (Appendix A) b) Brazil tests - Simultaneous deployment of Mataki, Garmin Etrex and Garmin 60Csx devices, by MIA, whilst walking linear understorey forest transects, in order to compare the locational fixes attained under forest canopy and whilst moving, but in a supervised manner and c) Active fieldwork (simulated hunts) – A total of 164 GPS deployments (across all device types), which were made across 30 simulated hunts in forest areas controlled by 27 local communities, involving 41 humans and 48 dogs, although dogs were not present during every simulated hunt. Data were downloaded and checked periodically during active fieldwork in order to monitor device functioning.

During active fieldwork, all GPS devices were programmed to record a waypoint every 10 sec. In practice however, mechanical differences between devices meant that the frequency of waypoint recoding varied. For Garmin devices, data capture reflected the device settings except in cases of device failure (for example because of low battery) or loss of satellite signal, which were uncommon. Igotu devices only succeeded in recording a waypoint every 18 – 30 sec, even when functioning normally. Mataki devices were programmed using the “*setgps*” function to (i) wait 60 sec after being initially turned on in order to acquire satellites; (ii) then search indefinitely for satellites; (iii) then, once satellites had been acquired, to record waypoints for three seconds; (iv) then sleep for 10 sec; (v) and finally search for satellites again and repeat until turned off. In practice, Mataki devices recorded a run of four waypoints, one every second, with gaps of 16 – 20 sec in between. Sampling frequency is known to be positively correlated with estimated movement distance (Mills *et al.,* 2006) and therefore devices with a lower data capture rate are anticipated to underestimate the distance travelled. In order to account for the aforementioned discrepancies between device data capture rate, it was necessary to use a restricted dataset, whereby only the first waypoint recorded per minute per device, was utilised (where a restricted dataset was used, this is indicated in the methods).

Due to concerns over device reliability (Appendix A) and in order to directly compare different types of device, during active fieldwork, two devices were deployed per surveyed individual. Human hunters were given the larger, heavier and more expensive Garmin 60Csx devices (paired with a Mataki device) as they were deemed too cumbersome to be deployed on all but the largest dogs and they are too valuable to risk losing. Robust dogs were fitted a collar with a Garmin Etrex device, paired with a Mataki device. Smaller dogs were fitted a collar with two Mataki devices. Initially, Igotu devices were also deployed alongside Garmin and Mataki devices. During routine data checks of devices carried out whilst conducting active fieldwork, it became evident that Igotu devices consistently failed to acquire satellite signal and capture locational data when under dense canopy. Although this did not constitute a static, supervised and controlled test, the obvious inability for Igotu devices to capture data under field conditions forced us to discontinue their use prematurely.

Hunting dogs in our study regions are known to run through dense vegetation and streams. Therefore before each simulated hunt, in order to protect GPS devices, makeshift waterproof housings were created. Devices were wrapped in three plastic bags, which were taped shut and attached to dog collars using cable ties and duct tape. Cable ties were then clipped short and taped over to avoid irritating the dogs (Appendix B). Human hunters were given the devices in two layers of plastic bag, taped shut. These were kept in pockets or backpacks during each simulated hunt.

Domestic dogs used in simulated hunts in our study regions, whether true-bred hunting dogs (locally named *cachorro paulista*) or mixed-breed dogs (locally *vira-lata*) are approximately the stature of a harrier hound or foxhound (Appendix B) and weigh ~ 18–30 kg. Animal welfare guidelines (American Society of Mammalogists, 1998) dictate that mammals should ideally not be encumbered with devices (including harnesses) weighing more than a fifth of their bodyweight (up to a maximum of a tenth). As our heaviest GPS collar setup, weighed less than 250g, it was well within acceptable limits even for the smaller dogs.

The support and goodwill of local communities was essential for this project. During meetings with community leaders and other members, it was explained that we wished to test new GPS devices and use hunters and their dogs to map the hunting grounds in proximity to communities. In order to avoid either making community members uncomfortable, or encourage an activity that is perceived to be problematic, we (1) sought community members that were experienced hunters and ideally those who regularly used dogs; and (2) explained that their activities would be deemed simulated hunts and mapping exercises and that anyone who wished to participate did not need to hunt, or even carry a shotgun. For this reason, their activities are referred to as "simulated hunts" or "surveys" rather than "hunts". The identity of local communities and participants in this study were anonymised as agreed prior to field deployments.

MIA was present at the start of every simulated hunt in order to program, prepare, house and attach every device and record the departure point. Before every simulated hunt, the number of people, fire weapons, and dogs of both types were recorded. After simulated hunts, if the participants were comfortable to share the information, a record was made of the number of animals killed or collected. We initially intended to accompany every simulated hunt in order to make notes on broad habitat categories and dog behaviour. On the two simulated hunts attended early in the study, some participants asked for prescribed directions using a GPS unit. We therefore did not accompany subsequent surveys in order to avoid unduly influencing their spatial features.

5.2.3 Local interviews

Interviews were conducted in Portuguese by the authors and without the aid of translators. Interviews were recorded using a structured questionnaire and a Dictaphone, and cross-checked for accuracy. Interviewees were reassured that data would be kept anonymous and confidential. Interviewees were not paid, but some were participating in paid work such as camera trapping at the time of interviews. During two field seasons undertaken in 2013 and 2014, a total of 78 interviews were conducted, with a total of 151 respondents at 59 local communities or urban neighbourhoods (hereafter, *communities*). Interviews addressed a broad range of topics related to livelihoods, hunting and forest fauna. Time constraints meant that it was not possible to ask every interviewee every interview question. For methods relating to interviews that focussed on crop raiding of agricultural plots and encounters with forest fauna, see Chapters 3 and 4, respectively.

Hunting dogs were mentioned, either by the interviewer or respondent, during three separate questions in the course of the aforementioned interviews. During 74 interviews (57 communities), interviewees were asked (1) "In general, in the area near to your community, is the hunting easier now than it was in the past?" and (2) "In your opinion, what can be done in order to ensure that there will always be sufficient game to hunt?" Additionally, (3) during 76 interviews, respondents were asked about the prevalence of the ownership of hunting dogs. The precise formulation of this question was altered between field seasons, as follows. During the 39 interviews conducted in the 2013, interviewees were asked "Do you personally own any hunting dogs?" These data were not used in the assessment of the prevalence of hunting dogs, as it was felt to be intrusive and potentially unreliable. During 37 interviews conducted in 2014, each in separate communities, interviewees were instead asked "Are there any households in this community that own dogs which are used during hunts (even if only rarely)?" and "Are there any households in this community that own bred hunting dogs?"

5.2.4 GPS data processing and GIS

All spatial data extraction was conducted using ArcGIS (v. 10.3). All data were projected into the Albers equal area conic projection. Waypoints were compared to ensure that devices were synchronised for each simulated hunt. The start and endpoints of every simulated hunt were specified as the points at which the group (whether dog and master or hunter alone) left and re-entered the central community or homestead. All waypoints before the start and after the end of simulated hunts were deleted.

The two study regions were classified into five landcover types: (a) permanent water bodies, (b) deforested land, (c) natural nonforest vegetation (including areas of *campina* and *campinarana*), and (d) primary upland and (e) low-lying forest using data from INPE PRODES, 2009, Global Forest Change (GFC: Hansen *et al*., 2013), RADAMBRASIL (Veloso, 1982) and the Instituto de Conservação e Desenvolvimento Sustentável Amazonas (IDESAM). PRODES land cover data were used to validate against GFC deforestation data (see chapters 2 and 3). In the Juruá region, the low-lying forest class corresponds to white-water *várzea* floodplain forest. In the Uatumã region by contrast, the low-lying forest class corresponds to both the small proportion of black-water floodplain *igapó* forest, and to the distinctive band of paleo-floodplain largely to the North and East of the Uatumã River (Amazonas, 2008).

For accompanied simulated hunts, the point at which the group started to travel overland was recorded using a GPS device. For unaccompanied simulated hunts, the routes taken were inspected against ESRI basemaps to determine where the group travelled by river and overland. For this purpose, we used (a) the aforementioned habitat classification, (b) a map of perennial streams combining data from the IBGE (2008) "*hidro tot linha*" shapefile and the Hydrosheds hydrographic dataset (Lehner and Grill, 2013a), and (c) field notes and tracklogs accumulated during two years of fieldwork.

The elevation of GPS waypoints recorded at every simulated hunt, relative to the main adjacent river, was calculated following Rennó *et al* (2008) using 1 arc-second (30-m) SRTM data (Jarvis, *et al*., 2008). Raw elevation is inappropriate due to landscape-wide elevational gradients. There are 24-m and 22-m elevational differences between the ends of our Juruá and Uatumã study landscapes, respectively, and a roughly 65-m elevational difference between study regions. To calculate the elevation of the river in proximity to each simulated hunt, a point shapefile of start locations was snapped onto a polyline of the main rivers. A buffer of 500m around each snapped point was then created and the lowest elevation within the buffer was used. The buffer was used to ensure that the true elevation of the river would be captured, rather than the nearby banks. The relative elevation per GPS waypoint was therefore the elevational difference between the waypoint itself and the corresponding point on the main river.

The distance between the survey community/homestead and the nearest town, was calculated as follows. A GPS waypoint was recorded at the centre of all surveyed communities and homesteads. A transport network accounting for all main rivers, tributaries, known navigable perennial streams, roads and known tracks in the vicinity of all surveyed communities was constructed from GPS track-logs taken over successive fieldwork years. Network Analyst was used to calculate the Manhattan or “transport” distance between communities and towns across both study regions. Having identified the town with the shortest Manhattan distance to a given community, the Euclidean distance between them was then calculated, providing a “hybrid” distance (see Chapters 3 and 4).

The number of households per community was recorded using (1) interviews conducted during this study, (2) Projeto Médio Juruá interview database, and (3) The Sustainable Forest Association (FAS) community census. Although our data is more recent, we were interviewing community members rather than conducting a population census. Mean values per community were used. The number of households per urban centre was calculated using IBGE (2007) census data.

Hybrid distance and urban population were combined into a single variable, the urban proximity score. This was calculated as the urban population, divided by the square root of the hybrid distance to a given community. More complex urban proximity indices (see Chapter 2) were previously devised and used, but our study landscape is more simple in this chapter and alternative urban proximity indices are highly correlated.

5.2.5 Statistical analysis

All statistical analyses were conducted in R (2.15.1). Collinearity between independent variables was tested for using Spearman’s Rank, Kruskal-Wallis and Wilcoxon Rank Sum tests. Where explanatory variables had bivariate Rho >0.70 or $p < 0.05$, they were modelled separately. Data distributions and relationships were inspected using histograms. For count data, Poisson models were attempted and where overdispersion was uncovered, Negative Binomial models were used. Variables were scaled to enable models to converge and aid comparison of variables. The ‘best’ models were selected based on their Akaike's weights (wAICc) and the ΔAICc, corrected for small sample sizes. We considered models with ΔAICc<2.0 and wAICc>0.1 as equally plausible to explain observed patterns (Burnham & Anderson, 2003, Bolker *et al.*, 2009). Where multiple plausible models were retained, they were weighted and averaged using the “*model.avg*” function in the R package *MuMIn*. We report coefficients and adjusted standard errors along with p-values per explanatory variable to aid interpretation (for further discussion, see Chapter 4).

5.2.6 Device comparison

As a measure of device reliability per simulated hunt, the number of minutes in the restricted dataset for which each device recorded a waypoint was used. In order to investigate the effect of device type on the proportion of each hunt captured, a negative binomial GLMM was created, in which the number of minutes recorded per device was the dependent variable and the log of the total number of survey minutes was an offset variable. Explanatory fixed effects were (1) the number of minutes spent in old-growth forest of any type, which was recorded by the device with the highest data capture rate per simulated hunt; (2) the mean relative elevation of the simulated hunt; (3) whether the device was given to a human or deployed on a dog; and (4) the type of device. The survey date and the individual ID were specified as nested random effects.

In order to assess the accuracy of different types of device, unrestricted data from paired devices (those deployed on the same individual) used both during simulated hunts and Brazil tests, were compared. Only waypoints recorded by paired devices during the same second were compared. The Euclidean distance between all paired points was extracted in ArcGIS.

5.2.7 Characterisation of simulated hunts

In order to describe and compare simulated hunts, the restricted data from only the device that captured the highest proportion of the entire simulated hunt was used (the lowest percentage for any simulated hunt was 94.6%). The mean relative elevation above local drainages, total distance travelled, farthest point travelled from the community/homestead, and the percentage of both time and distance spent travelling by river and overland and in each habitat category, were extracted in a GIS for each simulated hunt. In order to compare the total distance travelled and the number of bred hunting dogs used during simulated hunts (a) between study regions and (b) between simulated hunts that started from towns and those that did not, GLMMs were initially attempted, to account for data nestedness. GLMMs did not converge however, due to the sparsity of the data. Data were therefore averaged per community and nonparametric bivariate (Wilcoxon) tests were performed. Multiple statistical comparisons were made simultaneously on the same dataset, thereby introducing a multiple comparison problem and the potential for an inflated false discovery rate. A Bonferroni correction was applied in order to reduce the false discovery rate. Despite its widespread use, the Bonferroni correction is known to be overly conservative (Armstrong, 2014). Due to the sensitive nature of and potential behavioural biases inherent in our study, a conservative approach is appropriate and a reduction in type I errors, compensates the inflated risk of type II errors.

5.2.8 Comparison of dogs and humans during simulated hunts

In order to compare dog and human hunters during simulated hunts, only the overland proportion of the hunt was considered, thereby excluding periods when humans and dogs travelled together in canoes. To ensure data were comparable, only the 37 Garmin device deployments that captured over 90% of the overland proportion of the simulated hunt were used. When comparing the distances travelled, restricted data were used. Data were averaged per community and a paired Wilcoxon test was performed.

In order to ascertain to what degree dogs deviated from the locations used by human hunters, the unrestricted GPS data of human hunters were converted to polylines and merged per simulated hunt. The Euclidean distance from every dog waypoint to the nearest human track was then calculated. These distances were separated into three distance categories. Any points closer than 11 m are considered to be potentially adjacent to or using the same path used by humans, due to positional inaccuracy and coregistration error. Points between 11 and 100 m are considered sufficiently close to enable humans and dogs to easily communicate, whilst points farther than 100 m are considered far enough that communication between humans and dogs begins to become problematic in a dense forest. To determine if purpose-bred hunting dogs travelled farther from human tracks than other dogs during simulated hunts, a Gaussian GLMM with a log link was created, with the distance to the nearest human track as the dependent variable, the type of dog as the only fixed effect, and the survey location and dog ID as nested random effects.

5.3 Results

5.3.1 Attitudes to hunting with dogs

Of the 37 communities surveyed, 23 owned dogs that were occasionally used during hunts, nine of which had bred hunting dogs. Additionally, as reported in Chapter 3, semi-subsistence agriculturalists in the Juruá region frequently use dogs in order to suppress crop raiders in their agricultural plots. During 10 interviews, respondents expressed negative opinions about hunting with dogs. These included “I do not hunt with dogs, because they scare animals away” (N = 3), “Hunting is more difficult now / was more difficult before, because of hunters with dogs” (N = 5), “we should prohibit people from hunting with dogs” (N = 3), and “animals do not return to places from which dogs have chased them” (N = 2). Other than confirming their use either during hunting or to protect agricultural plots, no respondent expressed positive attitudes towards hunting dogs. One interviewee reported that their community incurred high consistent crop losses to collared peccary herds, until they employed a professional hunter with dogs from a nearby community to kill and scare them away. The intervention was so effective that they later acquired hunting dogs of their own.

5.3.2 Device comparison

Whilst in use during both simulated hunts and Brazil tests, waypoints recorded by Garmin Etrex devices deviated from Garmin 60Csx devices by an average of 10.2 ± 0.3 m. Mataki devices deviated from Garmin devices by an average of 21.4 ± 0.2 m, and Igotu devices deviated from Garmin devices by an average of 30.2 ± 2.2 m. When deployed during simulated hunts, Garmin devices captured on average 89.5 ± 2.9% of the hunt, whilst Mataki and Igotu devices captured 56.3 ± 4.0% and 36.7 ± 5.0% of the hunts, respectively. Garmin devices were therefore found to be both the most accurate (in terms of positional error) and reliable (in terms of data capture rate). Igotu devices were the least accurate and reliable and Mataki devices were intermediate.

Although it was impossible to determine the cause of total device failure in most cases, common causes appear to include battery dislodgement or severing (Mataki devices especially), battery failure, accidental pressing of the power button (Garmin devices especially), and occasionally water intrusion. Igotu devices commonly lost satellite reception under dense canopy cover, whilst this occurred less frequently for Mataki devices, and rarely for Garmin devices. Models of device reliability (Fig. 5.2) reveal that device type was the strongest predictor of the proportion of the simulated hunt captured, though mean elevation, the amount of time spent in primary forest and whether the device was deployed on a dog, also had a negative influence.

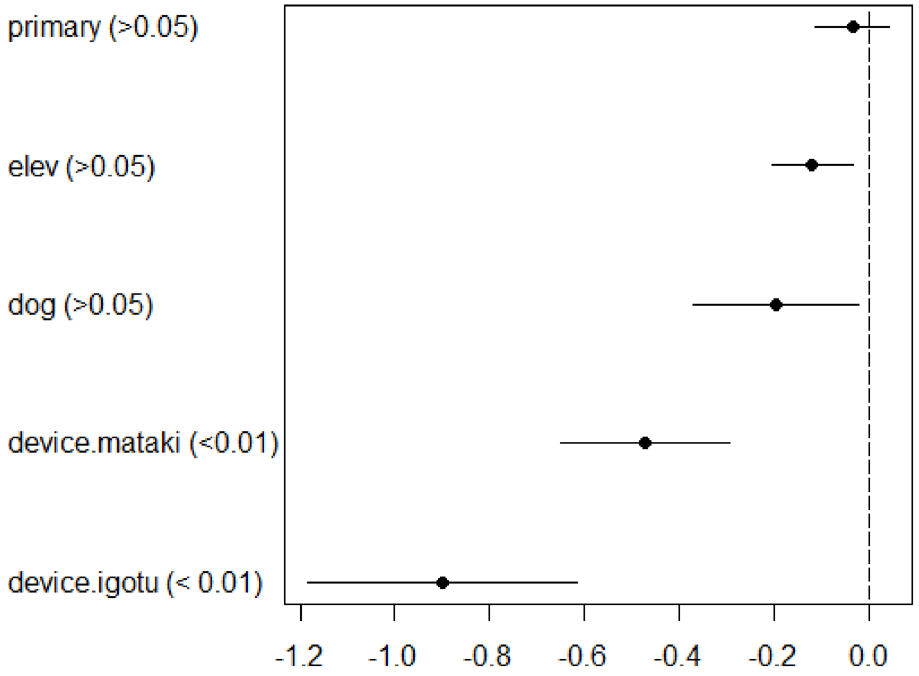

Figure 5.2: *Coefficients and adjusted standard errors of the variables retained in the best performing model of GPS data capture rate. Variable codes and associated P-values are indicated to the left of the plot, where primary = the length of time spent in either category of primary forest, elev = mean relative elevation, dog = devices deployed on dogs, device.mataki and device.igotu indicate the type of device used, where Garmin devices are the reference category.*

5.3.3 Characteristics of simulated hunts

Simulated hunt activity began at ~ 07:30h (Table 5.1) and lasted for 450 ± 25 min, covering 19.25 ± 2.4 km, including travel by river. Though 67.1 ± 5.4% of the distance travelled was overland, and several simulated hunts which began in communities situated in upland forest included no river travel whatsoever, the longest hunts, especially those from towns, included substantial (up to 91%) river travel. Whilst the urban proximity score does not covary with the distance covered during simulated hunts (Spearman's Rho = 0.07), those that began in towns covered a significantly larger distance (corrected $P < 0.05$) than those which began from outside towns. Distance travelled during simulated hunts did not differ significantly between study regions (corrected $P > 0.05$). The farthest point reached during simulated hunts was 5.52 ± 0.78 km from the origin community or household. Total distance travelled covaried with the farthest distance reached (Spearman's Rho = 0.80). Simulated hunts were attended by between one and four people accompanied by up to ten dogs, rarely with a bred hunting dog. At least one shotgun was always carried and frequently each person wielded a shotgun. Simulated hunts in the Uatumã region involved fewer people, dogs and guns and never included a bred hunting dog. The number of bred hunting dogs per simulated hunt differed significantly by region and between urban and non-urban locations (corrected P-values < 0.001 and <0.05, respectively).

After accounting for landscape-scale elevational differences, simulated hunts carried out in the Uatumã region were allocated to higher ground (45.6 ± 4.2 m above drainage) than in the Juruá region (25.7 ± 2.2m). Participants in simulated hunts spent the largest percentage of time in primary upland forest (54.8 ± 6.6%), followed by low-lying forest (23.5 ± 5.3%), on permanent water bodies (10.4 ± 2.8%), on deforested land (9.8 ± 2.1%) and on natural nonforest areas (1.6 ± 1.2%). Faster river travel meant that permanent water bodies represented a larger proportion of the distance travelled than the time spent. In the Uatumã region, the proportion of time spent in low-lying forest was roughly double that of the Juruá region.

Table 5.1: Overall characteristics of the survey days, where id = the survey/simulated hunt ID. Surveys 5a and 5b were conducted in two different, but overlapping locations, starting from the same community, on the same day. Surveys 25 and 28 were conducted in different locations and on different days, but with residents of the same community. Reg = study region, where jur = the Juruá region, uat = the Uatumã region, cm = an ID code per surveyed community or household, hhs = the number of households in the nearest community, urb = the urban proximity score, pp = the number of people who attended, gn = the number of guns that were taken, dg = the total number of dogs that were taken, cp = the number of those dogs that were bred hunting dogs, el = mean relative elevation, Start time = the time at which the group left the community or household, dur = the duration in minutes, %t = the percentage of time spent in a given habitat, defor = deforested habitat, nonf = natural non-forest, tf = primary upland forest, var = primary floodplain and low-lying forest, wat = permanent water body, land = overland travel, river = travel by river, far = the distance in meters from the community/household to the point furthest away, length = the total distance covered, perc = percentage of the survey captured by the best performing GPS device.

id	reg	cm	hhs	urb	pp	gn	dg	cp	el	Start time	dur	%t defor	%t nonf	%t tf	%t var	%t wat	%t land	%t river	far	length	perc
1	jur	m	80	75.31	3	3	6	4	15	07:56	570	8.8	0.0	0.0	79.6	11.6	41.3	58.7	15626	46658	100
2	jur	m	80	75.31	2	2	6	4	17	06:57	505	3.8	0.0	0.0	21.4	74.8	61.9	38.1	15672	42150	100
3	jur	c	113	152.98	3	3	9	4	24	05:44	1012	28.9	0.0	38.3	2.6	30.3	75.0	25.0	18099	67776	99
4	jur	w	36	22.38	2	1	4	1	34	07:48	437	19.1	0.0	80.9	0.0	0.0	100.0	0.0	6130	16295	97
5a	jur	o	17	16.87	3	2	3	2	34	07:25	492	0.8	0.0	83.3	12.0	3.9	89.1	10.9	5440	19168	100
5b	jur	o	17	16.87	2	2	3	0	29	07:25	492	0.8	0.0	82.7	12.6	3.9	81.0	19.0	3720	15345	100
6	jur	f	27	16.19	4	1	5	1	34	07:30	554	21.9	0.0	78.1	0.0	0.0	100.0	0.0	4909	18021	100
7	jur	d	19	15.22	2	2	2	1	22	07:36	450	31.2	0.0	61.2	7.6	0.0	100.0	0.0	2234	12385	100
8	jur	h	6	3.14	2	2	10	1	22	07:28	393	17.6	0.0	75.3	3.6	3.6	88.8	11.2	4845	19382	100
9	jur	x	8	2.88	2	1	2	0	18	07:40	469	30.6	0.0	47.4	17.1	4.9	89.3	10.7	8482	32058	100
10	jur	y	14	3.00	2	1	2	0	33	07:42	311	9.4	0.0	90.6	0.0	0.0	100.0	0.0	3018	10453	100
11	uat	aa	11	4.32	2	1	2	0	43	07:58	559	0.0	0.0	62.9	20.8	16.3	61.2	38.8	11285	31702	100
12	uat	t	18	2.38	1	1	3	0	74	08:31	428	0.0	0.0	57.1	41.9	0.9	100.0	0.0	5099	13423	100
13	uat	z	96	4.71	1	1	1	0	26	07:47	491	16.3	0.0	0.0	57.6	26.1	80.2	19.8	4497	16461	100
14	uat	k	8	3.97	2	2	2	0	38	07:56	425	6.8	0.0	44.1	45.8	3.3	58.6	41.4	2384	10715	100
15	uat	s	12	5.50	1	1	0	0	28	07:52	478	0.0	0.0	0.0	93.7	6.3	86.2	13.8	5148	20755	100
16	uat	j	20	5.13	1	1	1	0	55	08:08	419	19.9	0.0	80.1	0.0	0.0	100.0	0.0	2098	11030	100

id	reg	cm	hhs	urb	pp	gn	dg	cp	el	Start time	dur	%t defor	%t nonf	%t tf	%t var	%t wat	%t land	%t river	far	length	perc
18	uat	u	8	5.76	2	1	0	0	83	08:02	410	1.2	0.0	98.0	0.0	0.7	93.6	6.4	3378	10694	100
20	uat	l	9	14.04	2	2	0	0	48	07:27	449	5.8	0.0	92.9	0.0	1.3	100.0	0.0	2685	11973	100
21	uat	i	16	6.48	1	1	1	0	61	08:14	420	2.4	0.0	89.8	0.0	7.9	96.9	3.1	2512	12062	100
22	uat	g	4	6.56	1	1	1	0	27	06:40	456	17.5	0.0	0.0	72.1	10.3	88.8	11.2	1855	11877	100
23	uat	a	5	6.16	2	1	1	0	82	07:22	414	2.4	0.0	90.1	0.0	7.5	84.6	15.4	2202	13363	100
24	uat	v	12	6.12	2	2	3	0	25	07:51	296	3.8	31.7	0.0	51.5	13.0	83.7	16.3	3224	13608	99
25	uat	r	18	5.93	1	1	0	0	34	07:44	143	0.0	14.7	16.1	59.4	9.8	80.6	19.4	2143	7127	100
26	uat	e	7	4.84	1	1	0	0	30	07:55	347	0.0	0.0	0.0	70.2	29.8	79.0	21.0	4345	19344	100
27	uat	q	6	4.56	1	1	0	0	38	07:38	448	1.1	1.6	67.1	30.2	0.0	100.0	0.0	5416	14734	100
28	uat	r	18	6.02	1	1	0	0	43	07:22	449	0.7	0.0	88.8	3.8	6.7	72.9	27.1	3475	14010	100
29	uat	b	4	7.14	1	1	0	0	36	08:10	392	38.5	0.0	37.0	0.0	24.5	72.2	27.8	2436	7829	100

Participants chose to use existing paths where these were available, including trails created for logging, and linear transects for petroleum exploration and wildlife surveys (N = 7). Of the simulated hunts where participants disclosed their hunting offtake, 59.1% made at least one kill, with prey items including (from the most to least frequent) tortoise, collared peccary = greater long-nosed armadillo, agouti = tinamou = red brocket deer, and curassow.

5.3.4 Hunting dogs and humans

Considering the overland proportion of simulated hunts only, dogs did not often deviate greatly from their masters (Fig. 5.3a). Using data from only Garmin devices, the mean deviation of dog waypoints from human tracks was 7.9 ± 0.1 m. However, certain dogs occasionally made further forays from their owners (Fig. 5.3b). Bred hunting dogs ventured significantly farther from human tracks than other dogs ($p < 0.001$). Humans travelled on average 11,370 ± 900 m overland per simulated hunt, a distance shorter than their accompanying dogs ($p < 0.05$), which on average travelled 12,885 ± 1086 m.

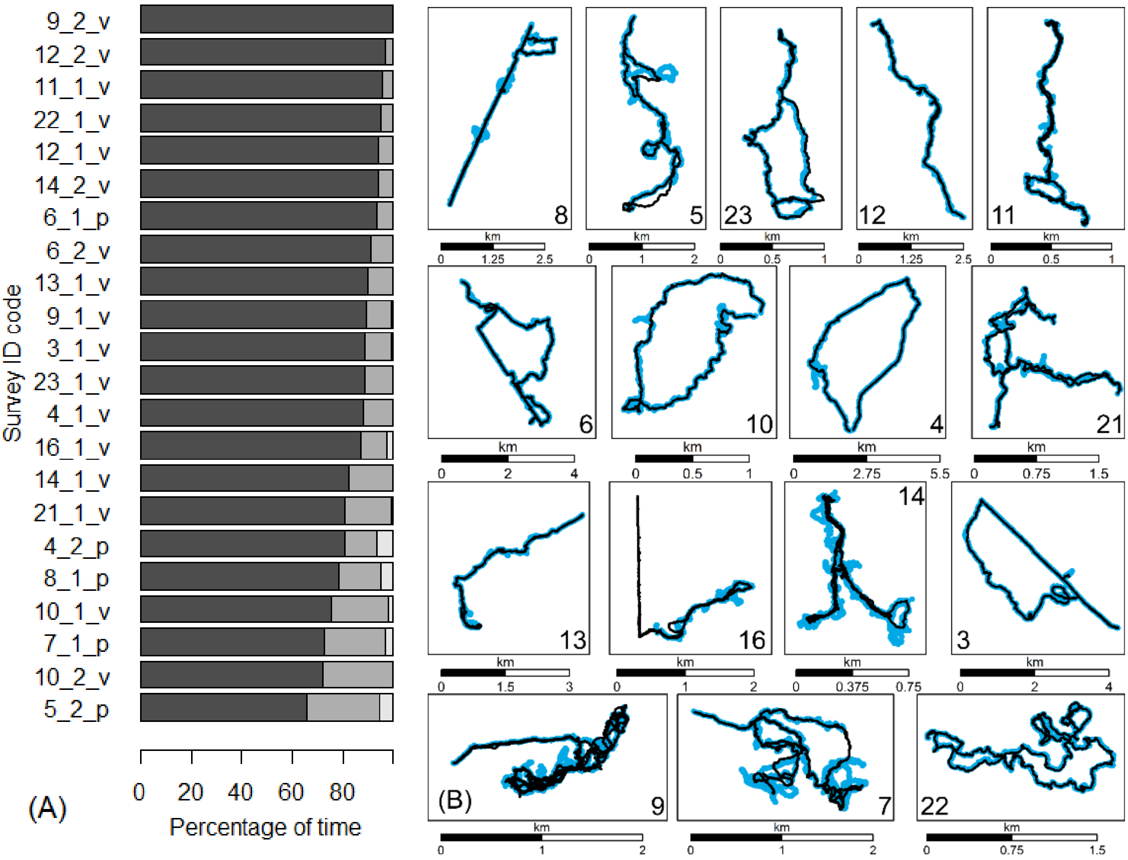

Figure 5.3: Percentage of time individual dogs spent at different distances from human tracks during the overland portion of simulated hunts (A). The colour of stacked horizontal bars represents the distance category (black: <11m, dark grey: 11-100m, and light grey: >100m). Survey ID codes are indicated on the left of each bar, including the ID of the dog and whether the dog was a bred hunting dog or not (p or v, respectively). Panel B shows the degree of overlap between humans and dogs during the overland proportion of simulated hunts. Human tracks are displayed as black lines and dog waypoints are blue overlapping circles. Only Garmin devices and hunts for which >95% of the terrestrial portion of the human survey was captured were used for this comparison. Panels are numbered according to the survey ID.

5.4 Discussion

5.4.1 Comparing devices

Field testing proved that Mataki devices are small and light enough to be an unobtrusive means of recording the spatial activity of humans and their hunting dogs. Though not as reliable (in terms of data capture rate) or accurate (in terms of positional error) as larger commercial GPS units, they functioned well despite being housed inexpensively and attached to hunting dogs ranging through thick undergrowth and streams and under dense forest canopy. They outperformed Igotu devices, which although small, light, simple, inexpensive and robust, did not reliably record spatial data under forest canopy. Mataki devices, unlike commercial GPS devices, required specialist hardware, software and training in order to charge, program, use and download data from, but their high degree of customisability and programmability easily offset these issues. These devices would be best suited for researchers (a) whose study species are fairly small (~ 1.5 kg), requiring small and light GPS devices; (b) whose study species range over a relatively large area, such that the loss of some fine-scale spatial resolution is acceptable (c) who have specialised data capture needs, best met by custom programming; and (d) who are able to deploy multiple devices such that the loss of data through occasional device failure does not jeopardise the overall dataset. More robust housing and harness solutions would reduce the rate of device failure to some degree. During our study, hunting dogs were capable of carrying heavier, more accurate and reliable GPS units, which were important to enable finer scale comparison of human and dog movement patterns.

Our study did not test the accelerometer and inter-device communication capabilities of Mataki units. Accelerometer data, paired with spatial data, enables researchers to investigate patterns of behaviour such as the stalking and chasing of prey (Williams *et al*., 2014). Mataki devices have the capability of transmitting data between one another and to a base-station (Fayet *et al*., 2015). This is crucial for study species that are likely to pass a fixed point, but are difficult or problematic to recapture. In our case, this was not necessary as hunting dogs were always eventually recaptured.

5.4.2 Comparing hunters and dogs

Evidence for the additional disturbance caused by hunting dogs over humans was mixed. During simulated hunts, dogs travelled significantly longer distances than humans, though only ~13% farther. Dogs spent the overwhelming majority of hunts very close to the areas used by humans, though bred hunting dogs ventured farther from hunters than other dogs. During one simulated hunt, a bred hunting dog was lost and beyond earshot, presumably chasing prey, and was not recovered until the following day. The Mataki device attached to its collar revealed that it had travelled over 2km away from human tracks, and had ultimately returned to wait by the riverside.

This was an exceptional event during our simulated hunts, but hunters indicated that it is not uncommon.

Our characterisation of the disturbance caused by hunting with dogs is incomplete. Though we compared the spatial footprint of hunters and dogs on the same simulated hunt, we were unable to determine if hunts that include dogs are fundamentally different in character than those which do not. Though simulated hunts including dogs in this study were indeed longer than those without, this effect was confounded by regional and urban differences. Secondly, we did not investigate the spatio-temporal relationship between humans and dogs. Namely, we did not determine if dogs actively led simulated hunts, or merely followed humans. Additionally, though we investigated disturbance spatially, it was beyond the scope of this study to investigate the effect that hunting dogs may have on the terrestrial vertebrate fauna. In order to achieve this, one would need to compare the faunal assemblage in proximity to otherwise similar communities that hunt with and without dogs, or conduct a longitudinal study of the faunal assemblage in proximity to a community that introduces the practice of hunting with dogs. One would also need to compare the quantitative prey offtake and profiles of hunts with and without dogs. As hunting dogs target terrestrial species (Koster, 2009) and reportedly hinder pursuit of arboreal species (Descola, 1996) they may reduce hunting pressure on large arboreal primates, which are extremely sensitive to overharvesting (Peres, 2000). Lastly, we did not quantify the behavioural effect on hunting dogs of either wearing GPS units or of engaging in simulated hunts. Although our GPS collars were well within the weight range tolerated by hunting dogs, they may still have resulted in reduced activity levels (Brooks *et al*., 2008). Device placement is also important (Vandenabeele *et al*., 2014) and collars may have caused more fatigue than a harness system. As lighter GPS units were less accurate and were deployed on smaller dogs, it was impossible for us to determine if GPS weight significantly depressed dog activity levels.

5.4.3 Comparing simulated hunts

There were significant regional and urban/rural differences between our simulated hunts. Even with our small sample size, simulated hunts that began in towns involved much longer travel distances. Given that urban areas appear to depress the overall biomass of the assemblage of terrestrial game species in our study regions (Chapter 4), this could be interpreted as evidence of both wild meat commercialisation by professional urban hunters and their need to travel farther to access game stocks.

We treat these results with caution due to the biases inherent in studying a contentious issue like hunting with dogs. Three sources of bias are likely to influence the results of this study: (1) sample selection bias: those who agreed to participate in our study are unlikely to be a random subset of hunters that use dogs. Commercial hunters, for example, are at greater risk of prosecution by IBAMA, and are less likely to participate; and (2) the Hawthorne effect and social desirability bias: participants were likely to have behaved differently during simulated hunts than they would have during normal hunts, because they knew they were being observed. In particular, they may have deliberately travelled shorter distances and perhaps curtailed the activity of their dogs, aiming to downplay the extent of their hunting activity, because they may have perceived it to be both risky and socially undesirable.

These biases, though unmeasurable, influence our regional more than our urban/rural inferences. The smaller numbers of hunters and dogs that participated in simulated hunts in the Uatumã region may reflect the fact that those communities modified their hunting behaviour due to distrust (having had less engagement with researchers in general) rather than any real difference in hunting culture. By contrast, the longer distances travelled by urban hunters cannot be explained by the aforementioned biases, because one would expect that they are at greater risk of discovery by IBAMA, and more likely than rural hunters to deliberately engage in artificially short hunts. However, the fact that a substantial proportion of participants invited me to participate in simulated hunts and shared details of their offtake, provide a degree of confidence.

5.4.4 Future research and conservation implications

To minimise the influences of the aforementioned biases, and more reliably characterise the spatial behaviour of hunters and their dogs, one would need to spend a significant amount of time working closely with members of a small number of communities. However, the idiosyncrasies associated with particular communities would not permit one to broadly generalise from these results. In every study, there are tradeoffs between information depth and breadth. We aimed to replicate our study design across a wide range of communities in order to compare the spatial behaviour of many humans and their hunting dogs.

To inform conservation policy surrounding the use of hunting dogs, research is needed not only into their ecological costs, but also their social benefits. Chapter 3 indicates that domestic dogs are a key tool deployed by semi-subsistence communities to protect their manioc plots, which form the backbone of their livelihood strategy. Dogs are also known to ward off dangerous predators such as puma and jaguar. The increased food security and safety afforded by dogs may enable local communities to coexist more effectively with their biodiverse surroundings (Sepúlveda, *et al*., 2014). Effective agricultural defence against crop raiders may increase land-use efficiency, thereby reducing motivation to clear larger agricultural plots. Likewise, the repulsion of large predators may reduce the frequency of retaliatory killing (Gonzalez, *et al*., 2012). This is mostly conjecture, however, as very little research of this kind has been conducted anywhere in the tropics. Therefore, the behaviour of dogs when in proximity to semi-subsistence communities and agricultural plots, is as important to study as their behaviour during hunts.

5.5 Conclusions

Garmin GPS units were found to be the most appropriate for our study. Their ability to reliably and accurately capture fine-scale movement patterns during surveys was more important than their extra weight, though the effect of this encumberment on dog behaviour was not quantified. Mataki devices were reasonably reliable and accurate, but more fragile and required specialist hardware, software and training. Igotu devices, although small, light, simple and durable were inappropriate as they did not reliably or accurately capture data under closed forest canopy.

Surveys that began in towns involved more bred hunting dogs and covered significantly longer distances than did rural surveys. Surveys in the Juruá region involved more people, guns, dogs and bred hunting dogs than in the Uatumã region. These could be taken as evidence of both hunting-mediated depletion in proximity to cities and of region-specific hunting cultures. These conclusions should be treated with caution, however, due to the biases inherent in our study.

Though dogs covered more ground than humans during surveys, the difference was not as pronounced as initially anticipated. Dogs spent a large proportion of surveys in close proximity to human tracks, but bred hunting dogs tended to venture further.

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Appendix A: Device testing in the UK and Brazil

A preliminary test was conducted in Hatfield forest in the UK over two days using two Mataki devices and a Garmin 60Csx device in order to (a) become familiar with the device functions; (b) determine if Mataki devices were likely to function under canopy; and (c) determine which GPS settings were most appropriate. Mataki batteries proved unreliable, with four out of the five batteries not charging. The battery that functioned, however, succeeded in recording copious data for nine hours. Mataki devices were initially programmed to sleep for one second between 30 sec intervals recording waypoints. This was in order to ensure that the devices had sufficient opportunity to acquire satellites and record waypoints under dense forest canopy. The Mataki devices functioned well in the relatively sparse forest, but the initially trialled GPS and accelerometer settings resulted in very high rates of data capture, and it took over three hours to download the data from a device. This is undesirable in cases where multiple devices are deployed per day during fieldwork. Therefore during active fieldwork, device settings were modified as described in the Methods. The on/off button on one of the two Mataki devices trialled was wired incorrectly. These issues prompted MIA to test every battery before using them in surveys and to use multiple GPS devices per individual. However, the test showed that Mataki devices had the potential to record an entire hunt without running out of battery or memory.

An additional test was conducted at two separate locations during fieldwork. On each day, which involved walking several kilometres along small tracks through the forest to collect camera traps, two Mataki devices, two Garmin Etrex devices and a Garmin 60Csx device were all carried simultaneously by MIA. Data from these tests were only used to compare device accuracy.

Appendix B: Device deployment and housing

As several devices were deployed each day, it was crucial to be able to quickly charge multiple batteries simultaneously and also download data and program devices. Mataki devices were supplied with two base-stations, which could each be used to recharge one battery and were also required to program devices and download data. Therefore, Adafruit micro LiPoly USB battery chargers were used in conjunction with adaptors created by technicians at the University of East Anglia. These were connected to two iSound portable power max 16,000 mAh rechargeable battery banks, each with 4 USB slots. This setup proved indispensable in the field, as electricity was not readily available.

Figure 5.4: *Photograph displaying the preparation of GPS devices for use in surveys, where 1 = A laptop computer running putty scripts to upload Mataki data, 2 = Garmin Etrex100 devices, 3 = a collection of dog collars, pliers, plastic bags, cable ties and duct tape used to create device housings, 4 = Mataki batteries attached to custom-made adaptors and Adafruit LiPolly usb chargers, 5 = iSound portable power max 16,000 mAh rechargeable battery banks, 6 = Igotu GPS units with dedicated usb charging cables, 7 = Mataki base-station used to program devices, charge batteries and upload data, 8 = Mataki devices.*

Our makeshift device housing proved inexpensive and moderately effective. Collars never became dislodged from dogs and devices never became dislodged from collars. In two instances the Mataki battery connecting wire became dislodged during surveys. Dogs regularly submerged the entire housing during surveys and water penetrated the housing in only three instances. In one case, this appears to have caused device failure.

Figure 5.5*: Photographs taken during fieldwork, showing the stature of typical Amazonian hunting dogs of varying ages and degrees of cross-breeding.*

Figure 5.6*: Photographs of GPS units inside protective housing attached to dog collars fitted to dogs during simulated hunts.*

Appendix C: Device dimensions and operability

Mataki devices, (weighing 33g, dimensions 6.4 x 3.4 x 1.0 cm, including battery) were a comparable size and weight to Igotu devices (20g, 4.5 x 2.9 x 1.4 cm), but smaller and lighter than Garmin Etrex (142g, 10.1 x 5.3 x 3.3cm) and Garmin 60Csx (213g, 15.5 x 6.1 x 3.3cm) devices.

Garmin devices, which cost £75 and £300 for Etrex10 and 60Csx respectively, were unsurprisingly the most feature-rich, as they were intended to be used as navigation devices. Many Garmin features, including their map display, were superfluous to their use in this study as route-recording devices. Freely-provided Mataki devices, which incorporated an accelerometer, had intermediate feature-richness. Igotu devices, costing £40, were the least sophisticated, performing only the function of taking waypoints at pre-programmed intervals.

Garmin devices use conventional AA batteries. We were able to purchase such batteries even in remote Amazonian towns. Garmin devices also featured a graphical menu interface, which permitted operation and device programming when away from a computer and freely available software (Garmin Basemap) to enable the download and processing of data. Igotu devices feature a dedicated USB charging cable, single-button operation, easily interpretable LED status indicators and free software (@trip) for device programming and data processing. These characteristics meant that Garmin and Igotu devices could be powered and programmed when in the field, and the data they recorded could be downloaded without any specialist equipment or training. Mataki batteries required custom-made adaptors in order to be recharged via USB. Data uploading and device programming was achieved using straightforward code when attached to a computer via a base-station. Despite the provision by Mataki of user guides and training material, MIA found that device LEDs did not intuitively indicate device settings or problems when in use, making the diagnoses of mechanical errors challenging in the field. Mataki devices thus required specialist, custom-made hardware and training in order to be used.

Chapter 6: Concluding Remarks

6.1 The need for nuance

The conclusions of this thesis are broadly congruent with the conservationist critique of large-scale inappropriate infrastructural development and perverse government subsidies for colonisation and deforestation (Laurance *et al*., 2004), but diverge somewhat from the largely polarised existing literature regarding community extractivist use of tropical forest resources (Brandon *et al*., 1998; Schwartzman et al., 2000). Echoing the results of numerous existing studies, we found that at the regional scale, much of the anthropogenic disturbance evident in rural areas, is in fact driven or directly caused by non-rural, non-local factors and agents including urban centres (DeFries *et al*., 2010), colonisation policies (Peres and Schneider, 2012) and (especially transport) infrastructure (Peres, 2001). The depletion of game fauna was also found to be an urban-driven phenomenon (Bowen-Jones and Pendry, 1999). Cognisant of the hypocrisy of inveighing against infrastructural development in tropical regions, whose inhabitants deserve the improved standards of living these may afford, we agree with authors who advocate for a well-planned balance between infrastructure and environmental protection, which will bring the greatest possible net social benefits, with the lowest associated ecological costs (Margules and Pressey, 2000; Caro *et al*., 2014; Laurance *et al*., 2015).

By contrast, we find that much of the debate surrounding the extractive use of tropical forests, and surrounding hunting in particular, presents a needless false dichotomy between what may (exaggeratedly) be termed anthropophobic and anthropophilic approaches to conservation (although several authors have attempted to bridge these divides, for example Peres and Zimmerman (2001)). Our results suggest that a more nuanced attitude towards extractive communities is needed. In our study regions, we found that forest-dependent communities clearly do impact forest fauna, but equally that they do not eradicate it. The question "Do forest-dependent communities extirpate terrestrial game fauna?" should be replaced with "under what social, demographic, technological and ecological conditions, and to what degree, do forest-dependent communities cause net species-specific and assemblage-wide depletion of terrestrial game fauna, relative to a baseline of the absence of those communities?". This explicitly recognises that the presence of those communities may deter the still-greater ecological impacts of non-local agents. These approaches are becoming increasingly common, for example through the use of bio-demographic and bio-economic models (Damania *et al*., 2005; Levi, *et al*., 2011).

In the remaining section of this thesis, I briefly summarise the main findings of the four data chapters (this section will be largely without references as I am summarising the findings of this study), draw out a recurrent theme, present potential conservation strategies and indicate fruitful areas of future research.

6.2 Summary of key findings

In Chapter 2, we found that at the regional scale, urban centres, fluvial accessibility and terrestrial transport infrastructure drive different patterns of anthropogenic disturbance along cul-de-sac Amazonian rivers both directly and indirectly, by influencing rural population density. Non-fluvial transport infrastructure, for example roads, transformed colonisation and land-use patterns in otherwise inaccessible rivers. Even our conservative characterisation of hunting catchment areas, non-structural disturbance affected an area over 18 times larger than structural disturbance.

In Chapter 3, semi-subsistence agriculturalists in the Jurua region were found to bear a triple burden imposed by the ecosystem disservices of terrestrial vertebrate crop raiders including; (a) 5.5% direct annual losses to crop raiders; (b) the labour and opportunity costs required to protect agricultural plots against crop raiders and avoid estimated losses that would be an order of magnitude higher; and (c) reduced opportunities to plant more palatable manioc varieties. As agricultural production is the primary livelihood and hunting is deemed less significant, the potential gains of hunting crop raiders do not fully compensate crop losses. Households in more isolated areas, that are already socially disadvantaged, are precisely those suffering higher losses to crop raiders.

In Chapter 4, we found that evidence for the depletion of terrestrial vertebrates in proximity to semi-subsistence communities in the Juruá and Uatumã regions was mixed. Only a select few species, especially large-bodied, group-living species, were heavily depleted by communities. Although species-specific shifts in activity patterns in response to community settlements were not evident, diurnal species were less prevalent near to communities. Collared peccaries may be competitively released in the absence of white lipped peccaries. Urban centres exerted a landscape-scale impact, depressing the aggregate biomass of forest vertebrates. Areas close to perennial streams were especially vulnerable to hunting. Our evidence for hunting-mediated depletion is likely to (a) be conservative due to our sampling strategy, which runs against the landscape scale gradient of primary productivity, and (b) represents a “best case scenario”, due to the high local availability of alternative animal protein, which effectively protects game stocks by reducing hunting pressure in our study regions (Endo *et al.*, 2016).

In Chapter 5, open source Mataki devices were found to be of intermediate reliability and accuracy when used to characterise the spatial behaviour of hunting dogs and their masters during simulated hunts. Hunting dogs travelled only ~ 13% farther than their masters, which was less than anticipated. There is evidence that hunters based in urban centers travel significantly farther than rural hunters. Local attitudes towards hunting dogs were mixed; they were recognised to have deleterious impacts on wildlife, but were commonly used to defend against crop raiders.

6.3 Urban influence

A recurring theme throughout this thesis, has been the pivotal role played by urban centres both in the livelihoods of rural Amazonians and in the anthropogenic disturbance of forest biodiversity, at the regional, landscape and household scales (Pinedo-Vásquez and Padoch, 2009).

Regionally, urban centres were found to be a strong driver of whole-river rural population density. This is unsurprising given the economic, information, and social services centrality of urban centres in the lives of even remote ribeirinho households (Parry *et al*., 2010). These households are themselves an important driver of both structural and non-structural forest disturbance. Our analysis of anthropogenic disturbance in proximity to cul-de-sac rivers likely underestimates the impacts of urbanites, who are more financially able to make long-distance forays into river headwaters to extract NTFPs, especially forest game vertebrates. The impact of commercial hunters has been shown to be more devastating than that of subsistence hunters (Vega *et al*., 2013). Assuming relatively secure tenure and moderate discount rates, long-term subsistence local resource users are theoretically incentivised to conserve natural capital such as game or timber stocks, in order to continually benefit from the harvestable “interest” (Godoy *et al*., 2001). Urban commercial hunters, loggers and gold miners, however, who are not dependent upon the persistence of viable resource stocks in a particular location and who have alternative livelihoods, benefit from liquidating natural capital as efficiently as possible.

At the landscape scale, urban centres, rather than rural communities, were found to depress the aggregate biomass of both crop raiding and hunted species. This reinforces the notion that household location choice is a livelihood trade-off, in this case, between greater access to natural resources and greater access to market goods and services (Alonso, 1964). Urban or suburban households incur lower losses of their staple crops to vertebrate crop raiders, and therefore benefit from higher yields, lower labour input in guarding activities, and the opportunity to plant less chemically defended, more palatable varieties of manioc. However, as suggested by (a) the lower biomass of hunted vertebrates near towns; (b) the longer distances travelled by urbanites during simulated hunts; and (c) evidence that hunter catch-per-unit effort is negatively related to urban proximity (Endo *et al*., 2016), urbanites can less readily access terrestrial game meat. The continuing rural exodus in Amazonia, as well as our finding that rural population density is strongly influenced by access to urban centres, are testament to the fact that in the livelihood calculations made by the majority of ribeirinhos, the costs of losing access to plentiful natural resources are outweighed by the benefits of closer integration into markets and better access to goods and services. This household level decision-making process is in fact universal to the wider urban-to-rural-to-wilderness gradient worldwide, but particularly in tropical countries, thereby shaping many of the conservation and development challenges of contemporary times (Browder., 2002).

Brazil is currently facing a deep political crisis and related economic uncertainty. Even before the corruption scandals and economic slowdown that ejected the former President from public office, however, Brazil was already facing a crisis of environmental identity (Loyola, 2014). Many Brazilian progressive environmental policies are being undermined (Ferreira *et al*., 2014), and there have been continued legal calls to compromise the status of existing protected areas (de Marques. and Peres, 2015). Funding for environmental agencies has been substantially reduced and the much lauded federal Forest Code that requires a legal limit to deforestation on private properties has been watered down (Soares-Filho *et al*., 2014). Destructive infrastructure projects including the controversial Belo Monte dam and long distance road network expansion are ongoing (Laurance et al., 2001). These economic and political factors seem likely to result in both a further weakening of environmental legislation and enforcement (Campos-Silva *et al*., 2015, as well as a reduction in the extent of government welfare support.

These trends will likely strengthen the aforementioned influence of urban centres. Government welfare support, both through direct payments such as the Bolsa Familia, which our interview respondents identified as an important livelihood component, and through the provision of services such as digital classrooms in rural communities, have until now slowed the rate of rural abandonment and increased the rate of sedentarism. If this support is significantly diminished, then the rapidly growing rural population is likely to continue to urbanise. Although the direct pressures exerted by rural households is likely to decrease and land abandonment may result in forest regrowth, weaker environmental legislation and lower funding will further reduce the defensibility of protected areas, which are already chronically underfunded and under-staffed.

6.4 Conservation Strategies

In light of the aforementioned findings, what conservation measures could be taken to ameliorate biodiversity losses? Our study appears to have identified some “low-hanging fruits” which are promising conservation strategies.

At the regional level, our analysis of cul-de-sac rivers suggests that conservationists should continue to oppose expensive and ill-conceived mega-infrastructure projects and perverse subsidies, particularly in low-governance frontiers lacking land-use planning. Given the need for the Brazilian government to demonstrate judicious spending of tax revenue, uneconomic subsidies including the agricultural resettlement program which has driven unsustainable and unprofitable agricultural expansion at the expense of tropical forests (Peres and Schneider, 2012), should be opposed. Realistic cost-benefit analyses for infrastructure development including road-building, are as much a civic duty as an environmental imperative (Caro *et al*., 2014; Laurance *et al*., 2014; Laurance *et al*., 2015). The suboptimal placement of the Balbina reservoir, for example has wrought large-scale ecological damage despite modest energy generation (Fearnside, 1989; Benchimol and Peres, 2015), yet an expansionist hydroelectric development strategy for all steep gradient river basins of Brazilian Amazonia remains largely unopposed (Lees *et al*., 2016).

In the Neotropics, terrestrial vertebrate crop raiding species are generally disturbance-tolerant and of relatively low conservation concern (Parry *et al*., 2009), whereas large primates including woolly and spider monkeys are both extremely vulnerable to depletion via hunting offtake (Peres, 1990) and are not identified as problematic species. Furthermore, many *ribeirinho* communities are disinclined to hunt primates for cultural reasons (Mittermeier, 1987). This suggests that placing stronger legal restrictions on the hunting of the most harvest sensitive species whilst simultaneously loosening restrictions on the hunting of crop raiding species, would minimally impact local livelihoods whilst benefitting biodiversity. This strategy would likely be less successful in indigenous reserves where the hunting of primates is culturally important (Da Silva *et al*., 2005). Similarly, this strategy is not easily applicable in the Afrotropics, where endangered elephants and chimpanzees are also both problematic crop raiders and frequently cause injury and endanger human life (Thirgood *et al*., 2005).

A related strategy would be to simultaneously place stronger restrictions on the use of specially bred hunting dogs, whilst tolerating or encouraging the use of other domestic dogs. The benefits that domestic dogs bring to local communities in warding away dangerous large felids and chasing away crop raiders, should be recognised (Verdade *et al*., 2004), but equally these benefits can accrue without the ecological damage potentially wrought by bred hunting dogs.

Given the importance of fluvial accessibility to hunters, one conservation strategy may be to empower communities sited at the mouths of perennial streams (*igarapés*) to restrict the access of non-resident hunters. The success of this strategy would be highly region-specific however.

Hunting in the Juruá region, for example, often occurs when water levels are high and returns from fishing are poor (Endo *et al*., 2016). This is precisely the period when *igarapés* can easily be bypassed by travelling through the flooded várzea.

Conservationists must question whether active terrestrial game management in rural Amazonia is necessary, desirable, or even possible. The evidence from this thesis is not sufficient to conclude that rural communities are emptying the surrounding forests of terrestrial game vertebrates, though they are impacting large, vulnerable and ecologically important species. Adaptive management of game stocks would require both robust faunal monitoring and representative unhunted baseline sites to serve as a basis for comparison (Walters, 1986). These measures would be costly and administratively challenging, but beneficial in themselves in that they would potentially create wildlife refugia and actively engage local communities in the process of conservation. Radical new conservation programs may be less effective than reinvigorating existing interventions including ProBUC faunal monitoring, which have proven successful, but are underfunded (Ferraz *et al*., 2008).

As noted, terrestrial game species are harder to monitor and restrict access to than pirarucu in oxbow lakes or turtles on beaches, and their lower productivity entails that communities are unlikely to observe a direct and rapid benefit from protection. These difficulties and the fact that the availability of aquatic protein has apparently reduced the hunting pressure in our study regions, and may be responsible for relatively low wildmeat extraction rates in the Amazon basin (Fa *et al*., 2002), suggest that an indirect and holistic strategy holds more promise. Hunting does not occur in isolation, but is part of a complex web of livelihood activities (Coomes *et al*., 2004). The most effective means of protecting terrestrial game stocks, may in fact be to continue to focus on the sustainability of local fisheries. The limited resources available to conservationists may be best spent combatting illegal logging, gold mining and perverse commercial fishing practices such as discarding of low-value species (Ruffino, 2001). These practices create negative externalities felt by local communities (Biller, 1994), as they depress fish stocks, thereby driving unsustainable hunting.

Lastly, and on a related note, conservationists may need to focus more attention on the unsustainable practices of Amazonian urbanites who are shown in this thesis and in other studies, to be having a large impact on biodiversity (DeFries, 2010). Environmental education and enforcement are likely to be better per-capita value for money in urban areas due to their high population density. Amazonian rural population densities in many areas are currently generally well below the 1 person/km^2 level generally deemed to enable relatively sustainable subsistence hunting (Robinson and Bennett, 2013), therefore our current focus on rural communities may be misplaced.

6.5 Future Research

Throughout this thesis, numerous intriguing avenues were identified that it was not possible to fully pursue. Analyses of region-wide riverine disturbance could be strengthened by comparing patterns of anthropogenic disturbance across a wider spectrum of rivers, ranging from virtually uninhabited, to cul-de-sac, to road-intersected, and finally to a bead-chain pattern. Levels of anthropogenic disturbance are likely to vary far more strongly between these categories than within them and this would provide a clearer picture of the likely current trajectory of virtually undisturbed rivers. This would require a clear analytic framework in order to apportion data between rivers and a hydrological river-basin approach may be promising in this respect. Similarly, if historical demographic data were available, one could analyse the human-mediated evolution of disturbance along a set of rivers. Given the structured nature of the causal interactions in this system, a path analysis using a larger sample size may be preferable to GLMs. Lastly, studies of anthropogenic disturbance tend to either focus on large-scale demographic processes without distinguishing cultural differences (Laurance *et al*., 2002) or focus closely on the decision-making of a spatially restricted population sample (Pichón, 1997). If the spatial distribution of different cultural groups were known, then their different impacts could be compared (see dos Santos Silva *et al*. (2008) for a case study using remote-sensing image-mining to identify agents of deforestation).

During interviews with semi-subsistence agriculturalists concerning terrestrial vertebrate crop raiding many interactions between human livelihoods and both terrestrial and aquatic species, were touched upon, but could not be pursued. Crop protection and human-wildlife conflict mitigation strategies have been extensively studied in the Afrotropics (Nelson *et al*., 2003), where conflict with dangerous, but endangered megafauna is common. The fact that Amazonian crop raiders are smaller-bodied than their Palaeotropical counterparts, and generally neither very dangerous nor highly endangered, may explain why they have been less studied. Human-wildlife conflict mitigation strategies in the Neotropics are however important to study, partly because rural Amazonians are frequently attacked and killed by large felids, crocodilians and serpents (Neto *et al*., 2011), their fisheries are impacted by aquatic predators including river dolphins and giant otters (Rosas-Ribeiro *et al*., 2012), and their livestock is predated by felids, mustelids, eagles, and snakes (Silveira *et al*., 2008). It is also important because these conflicts often result in retaliatory killings of threatened species (Marchini, 2012). For these reasons, more detailed research should be conducted into the nature and effectiveness of strategies used by Amazonians to protect themselves and their livelihoods. In particular, in-depth assessments of the use of both hunting and domestic dogs should be made in order to fully elucidate both their importance and the damage they cause to tropical forest biodiversity.

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