6 · *Use and Overuse*

6.1 Introduction

The exploitation of wild animals for their meat continues throughout the tropics and subtropics. This is an activity of crucial importance that continues to buttress the food security and livelihoods of many millions of people (Chapter 1). Even at varying stages of transition to agriculture, modern hunter-gatherers still exploit animal populations for food (Chapter 1), being able to continue doing this if extraction is in balance with production. Likewise, numerous rural peoples still depend on wild meat, as we show in Chapter 2. Ensuring that supply matches demand for wild meat from those human populations still living in or near natural ecosystems remains a central question; we discuss the issue of sustainability in more detail in Chapter 5.

In this chapter we offer an overview of the impact of hunting on prey populations in the world's tropical and subtropical regions. We first present what estimates are available of wild meat extraction levels for areas where information exists, followed by a discussion of spatial patterns of wild meat extraction at a regional scale. We then focus on the existing evidence for how overhunting can reduce prey populations and change species assemblages. What drives wild meat exploitation is then discussed and we end the chapter by summarizing the evidence on the effects of anthropogenic faunal loss, or defaunation, on wider ecosystem processes and functions.

6.2 Global Wild Meat Extraction Estimates

Data on the biomass of animals harvested in different localities throughout the tropics and subtropics are generally rare, particularly for Southeast Asia. Most published hunting studies tend to concentrate on listing the animal species that are removed from a particular study area but often do not specify the number of animals or the biomass (kg) extracted per unit hunting area. This is because information on the numbers of animals hunted is often taken from hunter reports and hunting territories are not generally measured. However, from a compilation of studies, albeit relatively small, Robinson and Bennett (2004) examined the supply of and demand for wildlife resources across the rainfall gradient in relatively undisturbed ecosystems, generating estimates of the biomass of wild mammals (rodents, primates and ungulates) in evergreen wet and moist forests (rainforests), deciduous dry forest and grassland savanna. From these results, extraction rates were highest (744 ± 1,030 kg/km^2, n = 4 sites) in grasslands, followed by evergreen wet and moist forests (168 ± 193 kg/km^2, n = 14 sites) and lowest in deciduous dry forests (126 ± 150 kg/km^2, n = 4 sites). In evergreen wet and moist forest sites where human population sizes are available (from Robinson & Bennett 2004), the biomass harvested per person is positively correlated with rainfall (Fig. 6.1).

Information from 36 African rainforest sites compiled in Fa *et al.* (2005) show that from 40 to 12,168 carcasses are extracted annually per site (average 2,060 carcasses/yr per site or 240 kg/yr to 84,100 kg/yr), translating into a mean harvest rate per hunter of between 101 to 165

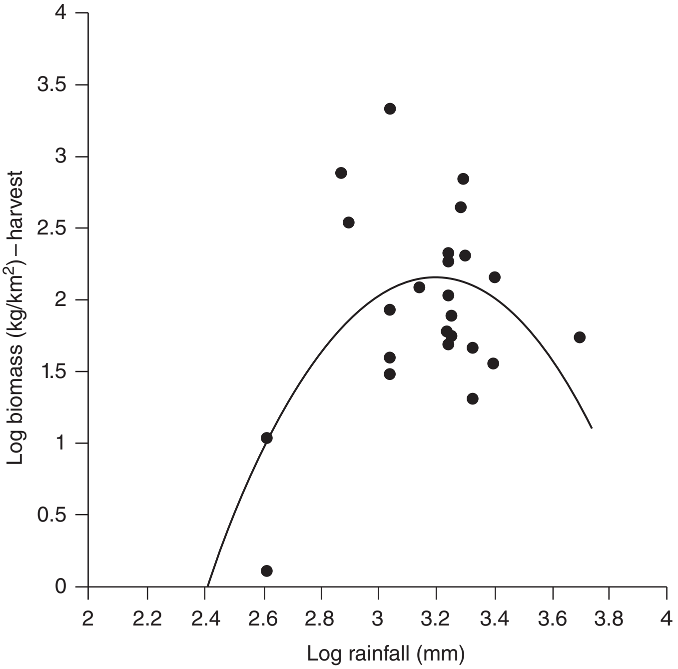

Figure 6.1 Biomass (kg/km^2) of ungulates, primates and rodents harvested in different tropical habitats in relation to rainfall (from Robinson and Bennett 2004; adapted with permission from John Wiley & Sons).

carcasses/yr and biomass of 946–1,610 kg/yr. Such variation in the number of carcasses hunted per year is a function of hunter numbers and provisioning conditions of each habitat. The impact of hunting intensity, forest structure and hunting history clearly influences prey standing biomass and the extraction potential in each habitat. But, even though habitat type and disturbance may affect animal numbers (see Chapter 2) there are major differences in populations of large-bodied vertebrates in hunted and unhunted Neotropical forests (Bodmer *et al.* 1997; Cullen Jr *et al.* 2000; Glanz 1991; Mena *et al.* 1999; Peres 1990, 1996, 2000; Wright *et al.* 2000), suggesting that the impact of hunters is paramount.

In all tropical regions where hunting of wildlife for meat occurs (Chapter 1), most prey animals are mammals, and among these the highest proportion is of ungulates (Coad *et al.* 2019). In a meta-analysis of hunting in Afrotropical forests in West and Central Africa, Fa *et al.* (2005) showed that as many as 71 mammal species were hunted in a total of 30 sites in 7 countries: 22 primates (5 families), 18 ungulates (4 families), 13 rodents (4 families), 12 carnivores (4 families), 3 pangolins, and 1 species each of elephant, hyrax and aardvark. For all sites pooled, ungulates (47%), followed by rodents (37%), were the most frequently taken taxonomic groups. Ungulates provided 73% in weight, while other groups significantly less. Small- (2.0–4.9 kg) and medium-sized (5–14.9 kg) species supplied more carcasses to the total kills (32.4% and 30.0%, respectively) than larger-bodied (15.0–99.9 kg) ones (21.6%). Large mammals alone made up 54.5% of total biomass extracted per year. Overall, the average estimated mammalian biomass extracted per year per site was almost 16,000 kg. Because most hunting is undertaken by non-discriminatory snares (where very few species, most of them primates, are shot), the relationship between the estimated average harvest rates per species correlated with body mass of the hunted groups. The smallest prey were arboreal species whilst the heaviest were almost exclusively terrestrial and a total of 32 out of the 36 terrestrial species were snared, whereas 13 of the 21 arboreal species were shot. The resulting pattern was a negative correlation between body mass and harvest rates for carnivores and ungulates, positive for rodents and curvilinear (inverted U-shape) for primates (Fig. 6.2). Smaller carnivores and ungulates but larger rodent species are therefore more susceptible to being caught in snares, whereas mid-sized primates are more likely to be shot. Smaller primates, mostly nocturnal (e.g. galagos) and larger ones (gorillas and chimpanzees) are rarely sought out by hunters, the former because of their lower cost-effectiveness and the latter because it requires

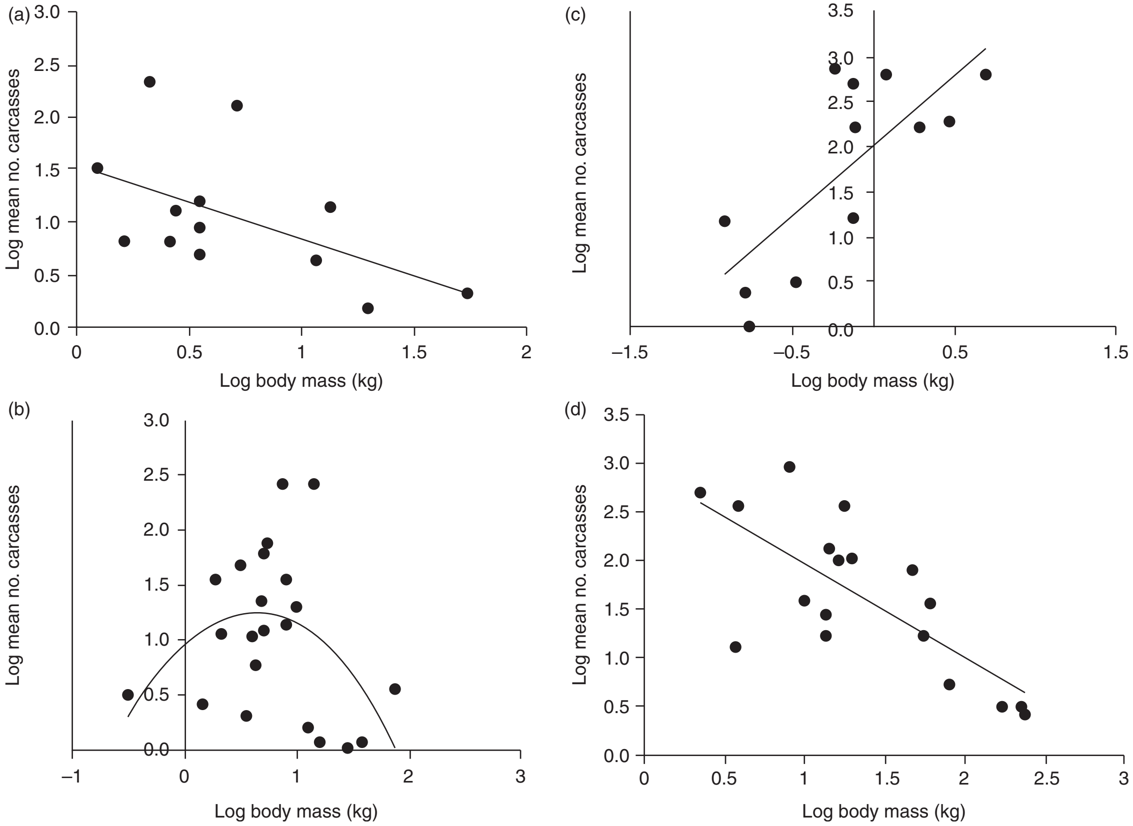

Figure 6.2 Regressions showing the relationship between species body mass and mean number of carcasses extracted per year of: (a) carnivores, (b) primates; (c) rodents; (d) ungulates. (From Fa *et al.* 2005; adapted with permission from PLOS Biology.)

more specialized hunting abilities to take down. Overall, there is some evidence that wild meat extraction, according to the data in Fa *et al.* (2005), is less driven by hunters choosing which prey to hunt, but by the hunting method employed.

As a consequence of mostly using snares and the effects of these as shown above, harvest rates are not correlated with the abundance of the species in the habitat except for ungulates (Fa *et al.* 2005). This can be explained by the fact that in West and Central African forests most of the terrestrial mammalian faunas are bovids (see Chapter 2), which are highly abundant particularly the smaller duikers, their larger densities saturating traps before other terrestrial species. In terms of which dietary categories of mammals were hunted in West and Central Africa, Fa *et al.* (2005) and later confirmed by Petrozzi *et al.* (2016) showed that frugivore–herbivores and frugivore–granivores were mostly impacted, both in terms of number of carcasses and biomass, with most harvested species being rodents and ungulates. Not surprisingly, the average number of hunters operating per 100 days (hunter presence in Fa *et al.* 2005) in a site is significantly positively correlated with biomass harvested. Biomass hunted is also highly correlated with the susceptibility of a species to be hunted, or hunter ease, in Fa *et al.* (2005), as a measure of the vulnerability of a species to hunting as determined by the size of the prey animal (since larger animals are more conspicuous), whether arboreal or terrestrial, and the species' speed of movement. Similarly, carcass numbers were not correlated with hunter presence, but were highly correlated with hunter ease, pointing to the overriding importance of vulnerability of prey species.

In a more recent meta-analysis of 82 studies on 254 mammal and 1,640 bird species from across the tropics, hunting was shown to be less intense for larger-bodied than smaller-bodied species of mammals, particularly among carnivores and frugivores, than for herbivores, insectivores and generalists/omnivores (Osuri *et al.* 2020). In the same study, body size was either unrelated or weakly negatively related among birds across disturbance types (hunting, forest conversion and forest degradation) and across most dietary guilds, with the exception of herbivore/granivore and carnivore species. The most significant generalization is that large forest mammals make up the bulk of the hunted biomass in most sites and these large-bodied species are the most susceptible to over-exploitation. Such vulnerability may not be only due to the size of the animal but also due to its behaviour, for example, living in social groups or loud vocalizations may make the species more easily found by hunters (Fitzgibbon 1998; Infield 1988). Nonetheless, extraction levels will logically correlate with the density of hunters operating in an area, thus if hunter presence is not too intense, adjacent large tracts of undisturbed forest can replenish exploited areas, restocking prey populations and therefore contributing to the sustainability of hunting (Fa & Peres 2001). But, heavy hunter presence, deforestation and habitat fragmentation in an area disrupts such source–sink dynamics (Novaro *et al.* 2000), leading to over-exploitation of animal populations. Often, large mammals and birds, which tend to disappear first, are frugivores (including frugivore–granivores, frugivore–herbivores and frugivore–omnivores) and important in seed dispersal (Abernethy *et al.* 2013; Wright *et al.* 2000). Their absence can have severe impacts on the long-term future of tropical forests.

6.3 Evidence of Sustainability

Published studies of the sustainability of extraction in tropical forests (Table 6.1), which have compared estimated productivity and offtake rates, show that in most cases hunting appears to be unsustainable. In most cases, more than half of the species considered in each study was unsustainably hunted; in situations where the number of species was low, more than 50% and up to 100% of these were unsustainably hunted. These figures attest to unsustainable extraction of wildlife in all circumstances where hunting has been studied. How representative these studies are cannot be assessed. Sustainability in most of the studies included in Table 6.1 has been measured using the Robinson and Redford (1991b) index, which has inherent problems (see Mayor *et al.* 2016; van Vliet & Nasi 2008a; Chapter 5) that may affect the results. Sustainable extraction is thus likely to occur in very remote locations, areas sparsely populated by humans, or beyond the influence and attraction of external markets. By contrast, locations such as ‘mature’ markets in Ghana (Cowlishaw *et al.* 2004) can still contain a number of sustainably hunted species, large rodents in particular, given that larger species have been overhunted and smaller species can be exploited for longer. Evidence that animal populations are impacted by hunting can be derived from population density estimates of target species have been suggested as an indicator of sustainability (see e.g. Cawthorn & Hoffman 2015; Chapter 5). This assertion is perhaps equivocal since it is expected that hunted areas will be lower in density but the decline in stocks may not reflect unsustainable use. Estimates of standing stocks of mammals in a large number of Amazonian localities that have been hunted to varying degrees clearly show that they are affected by hunting pressure and forest type (Peres 1999a; Fig. 6.3). Thus, it is not

Table 6.1 *Estimated sustainability and decline in population densities of mammals due to hunting (taken from Cawthorn and Hoffman 2015)*

Country/region – site	Main reason for hunting	Column I	Column II	Reference
Africa				
Congo Basin		60% (57)		Fa *et al.* (2002)
CAR, Mossapoula	Subsistence/trade	100% (4)	43.90%	Noss (2000)
Cameroon	Subsistence/trade	100% (2)		Fimbel *et al.* (1999)
Cameroon	Subsistence/trade	50–100% (6)		Delvingt *et al.* (2001)
DRC, Ituri I	Subsistence		42.10%	Hart (1999)
DRC, Ituri II	Subsistence		12.90%	Hart (1999)
Gabon, Makokou			43–100%	Lahm (2001)
Equatorial Guinea, Bioko	Subsistence/trade	30.7% (16)		Fa (1999)
Equatorial Guinea, Rio Muni	Trade	36% (14)		Fa and Garcia Yuste (2001)
Equatorial Guinea, Rio Muni	Trade	12% (17)		Fa *et al.* (1995)
Ghana	Trade	47% (15)		Cowlishaw *et al.* (2004)
Kenya	Subsistence/trade	42.9% (7)		Fitzgibbon *et al.* (1999)
Madagascar – Makira Forest	Subsistence	100% (5)		Golden (2009)
Latin America				
Brazil, 101 Amazon sites	Subsistence		90%	Peres (1999a); Peres and Palacios (2007)
Brazil, Mata de Planalto			27–69%	Cullen *et al.* (2000)
Bolivia	Subsistence	50% (10)		Townsend (2000)
Ecuador, Quehueiri-ono	Subsistence	30% (10)	35.30%	Mena *et al.* (1999)
Paraguay, Mbaracayu	Subsistence	0% (7)	53%	Hill and Padwe (1999)
Paraguay, Mbaracayu	Subsistence		0–40%	Hill *et al.* (2003)
Peru, Manu National Park	Subsistence	26% (19)		Ohl-Schacherer (2007)
South/Southeast Asia				
Indonesia, Sulawesi	Subsistence/trade	66.7% (6)		O'Brien and Kinnaird (1999)
Indonesia, Sulawesi	Subsistence/trade	74% (4)		Lee (1999)
India, Nagarahole			75%	Madhusudan and Karanth (2018)

Abbreviations: CAR = Central African Republic; DRC = Democratic Republic of Congo.
Column I: percentage of species hunted unsustainably (number of species studied). Sustainability indicators reported here are generally determined through the examination of the relationship between estimated productivity and off-take rates.
Column II: percentage by which densities of target species are lower in moderately to heavily hunted forests than in un-hunted forest.

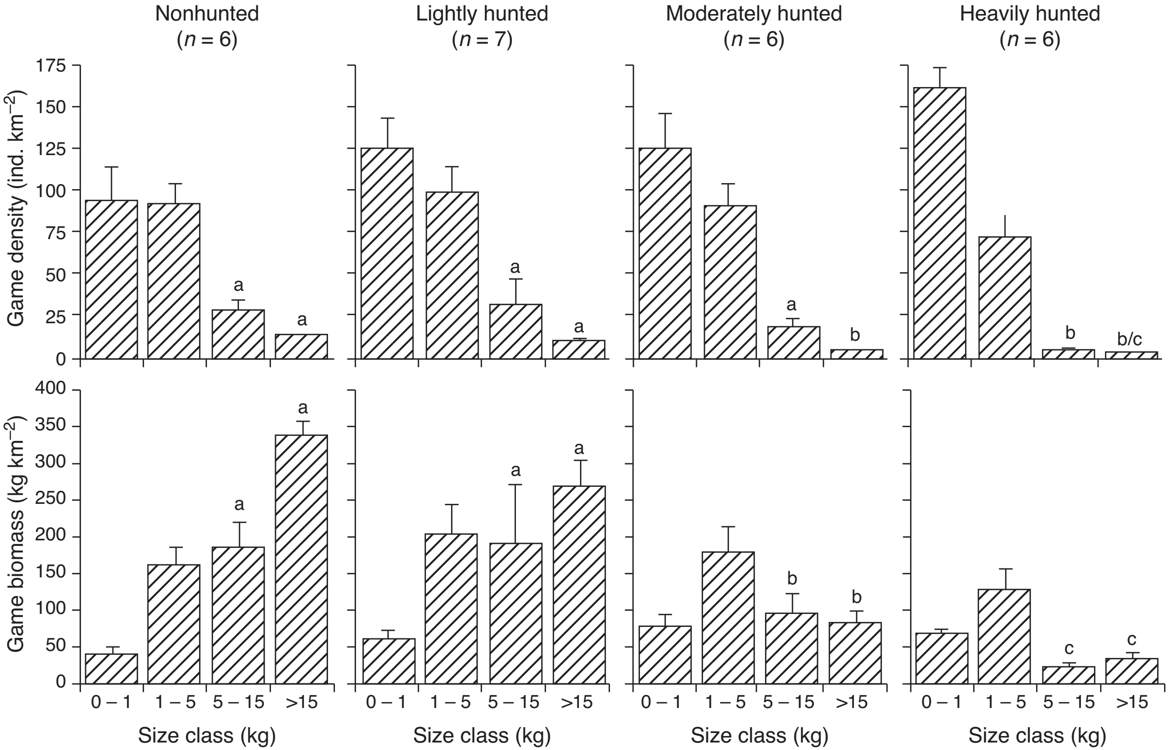

Figure 6.3 Total density and biomass (mean ±SD) of game populations in four different size classes subjected to varying levels of hunting pressure. For significant analyses of variance of log(e)-transformed density and biomass data, means are compared within each size class and across different levels of hunting; means that share the same letter do not differ significantly ($p < 0.005$) according to a Tukey multiple comparison test. (From Peres 2000a; adapted with permission from John Wiley & Sons.)

possible to determine whether these species assemblages have been hunted unsustainably or otherwise, since sustainability can only be determined as the difference between production and extraction.

6.4 Drivers of Extraction

Given the trends in human populations and infrastructure growth, impending large-scale degradation of ecosystem structure and content are underway in tropical forest regions. However, understanding what drives the ever-increasing extraction of wild meat, currently the most pervasive human activity in large forest blocks, is essential.

6.4.1 Wealth and Proximity to Wildlife Areas

Wild meat extraction patterns as described above are driven by a number of economic, social, geographic or other factors that reflect the scale of human reliance on wildlife. Brashares *et al.* (2011) point out that wild meat can be viewed as an 'inferior good' or a 'normal good'. As an 'inferior good', poorer, rural households would typically consume more wild meat than wealthier, urban households because wildlife provides a cheap and accessible source of food and income. In contrast, as a 'normal good', wild meat, like most household goods, would increase as household wealth grows. These two perspectives, although informative, oversimplify the reasons for wildlife consumption since there are a number of interacting and dynamic factors involved (Brashares *et al.* 2011). Overall, inhabitants of poorer rural areas have greater access to wildlife and the price of wild meat relative to alternative foods is lower. Using data across 2,000 households and 96 settlements in four countries in Africa Brashares *et al.* (2011) present evidence of the link between household wealth and wildlife consumption. Results from this study indicate that the least wealthy households in rural settings consistently consume greater amounts of wild meat (Fig. 6.4a), whereas wealthier households show higher rates of consumption in urban settings (Fig. 6.4b). The split between urban and rural settings, as suggested by Brashares *et al.* (2011), reflects considerable spatial variation in access to wildlife, as well as wild meat prices relative to those of alternative foods, and opportunity costs of time spent hunting, all of which are correlated with wealth measures. Conflicting results obtained in other studies may be due to the impact of the co-occurrence of spatial differences in wealth and wild meat consumption patterns.

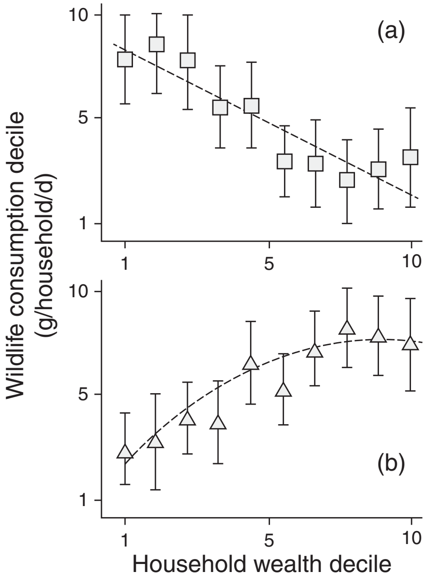

Figure 6.4 Household wealth is (a) significantly and negatively related to consumption for the 500 most rural households and (b) positively related to consumption for the 500 most urban households. (From Brashares *et al.* 2011; adapted with permission from the National Academy of Sciences, USA.)

Most available information on amounts of wild meat consumed relate to rural people (see Chapter 1) with only a few studies concentrating on urban settings (East *et al.* 2005; Fa *et al.* 2019; Wilkie *et al.* 2005). Comparisons between rural and urban wild meat consumption in Gabon showed that rural populations consumed significantly more wild meat (and less domestic meat) than did urban people (Wilkie *et al.* 2005). In a number of towns in Rio Muni, Equatorial Guinea, Fa *et al.* (2009) found that availability of wild meat differed substantially among localities, primarily depending on their location relative to forest areas. Despite these differences, overall meat intake was greater in wealthier households in all studied localities. However, because wealth distribution profiles differed significantly between sites, socio-economic conditions in the largest settlement, the city of Bata, influenced wild meat consumption in a distinct manner from the smaller, more rural sites. Reasons for this may be related to the fact that the substantially wealthier groups in Bata were consuming wild meat exclusively for prestige reasons. In contrast, wealth did not affect the likelihood of consuming domestic meats, and there was strong evidence that both site and wealth affected fish consumption: wealthier families were less likely to consume fish.

Until recently, urban consumption within the Amazon was not considered important and much of the emphasis had been placed on urban wild meat consumption in one city, Iquitos, in Peru (Bodmer & Lozano 2001). Based on this perception, for some time, urban wild meat consumption in Amazonia was regarded as negligible (Nasi 2001; Rushton *et al.* 2005). Recent studies suggest that this is not the case since there are significant city markets in the region where many wild animal species are sold for human consumption. For example, in the Brazilian Amazon well-established wild-meat markets have been documented in Abaetuba (Chaves Baía Júnior *et al.* 2009) and in two pre-frontier cities in the region (Parry *et al.* 2014). Estimates of about 473 tonnes of wild meat have been calculated as annually traded in a number of cities in the Amazonian tri-frontier (Brazil, Colombia and Peru) region according to Van Vliet *et al.* (2014). Although studies documenting sale of wild meat in urban centres in Latin America are mounting, factors affecting wild meat consumption and trade in this region are still largely undescribed in comparison to African cities (Fa *et al.* 2009). However, a few studies point to how the economic and cultural background of consumers in Amazonian cities, for example, affect how much wild meat is eaten (Chaves *et al.* 2017; Morsello *et al.* 2015). El Bizri *et al.* (2020b) found that in a study of six urban wild-meat markets in Amazonas state, a significant proportion (80%) of urban dwellers buy and consume wild meat. In Brazilian cities close to forest areas, Parry *et al.* (2014) showed that the poorest urban households hunt to obtain wild meat, whereas wealthier residents buy it. This is because hunting is the cheaper option for poorer people in cities, but also because the lack of formal employment, more common among this group allows them to spend more time in this activity. In some Amazonian cities, urban hunters profit from the sale of up to 97% of their game to closed markets (Van Vliet *et al.* 2015). According to a further study by El Bizri *et al.* (2020b) only a low number of urban residents declared hunting wild meat in the study, indicating that rural hunters are the most active supplying city markets. This is because hunters from rural areas in Amazonia are mainly subsistence hunters, but may sell part of their hunting yields, to generate money to buy urban goods, such as clothes and foods (Antunes *et al.* 2019). For instance, in the Peruvian Amazon, Bodmer and Lozano (2001) found that rural hunters sell around 7% of mammals hunted, whereas

Morcatty and Valsecchi (2015) found that around 21% of yellow-footed tortoises harvested by rural hunters in Amazonia were traded in urban wild meat markets. What is clear is that hunting wildlife for urban markets is a prerogative of rural inhabitants. The El Bizri *et al.* (2020b) study found that the proportion of rural inhabitants within a municipality was correlated with the proportion of inhabitants that declared consuming wild meat in cities, the reported frequency of consumption, and the prices per kilogram in the market. This pattern may be a result of the economic connectivity between urban and rural sectors in these municipalities. Thus, in municipalities where the rural population is larger, urban people are able to buy wild meat more frequently from rural people who hunt. Because these small cities are often isolated and only accessible by boat, domestic and processed products become more expensive due to higher transportation costs. As a consequence, wild meat prices are higher in small cities, where rural inhabitants outnumber urban ones, because trading in wild meat is one of the most prevalent and cost-effective activities in localities where agricultural commodities do not have a large local market and are uncompetitive due to high costs and long transportation times (Wilkie *et al.* 2016).

Wild meat extraction (and therefore consumption) is related to proximity to harvestable wildlife populations (Brashares *et al.* 2011). According to the data in Brashares *et al.* (2011) the effect of distance seems to disappear at 30 km or more, that is, consumption rates in settlements as close as 30 km to a wildlife harvest area were like those as far as 150 km away (Fig. 6.5a). Wild meat prices were cheaper around sites nearer to harvest areas, but higher in urban markets since having travelled some distance from its source after being sold to middlemen (Fig. 6.5b). From data for wild meat and domestic meat and fish in 52 markets Brashares *et al.* (2011) showed this effect (Fig. 6.5b). The price of wild meat relative to alternative meat also increased with increasing distances from hunting areas.

Because wild meat prices increase with proximity to urban areas, those hunters who harvest wild meat nearer cities should gain relatively more from selling their catch than those hunters in more remote areas. Consequently, hunters closer to cities are more likely to sell rather than consume their quarry. Brashares *et al.* (2011) showed that a high proportion (75–95%) of wildlife harvested in the settlements most isolated from commerce networks was consumed locally by the hunter's household or neighbour. In contrast, hunters who lived within 10 km of an urban market sold more than 80% of their catch to outsiders.

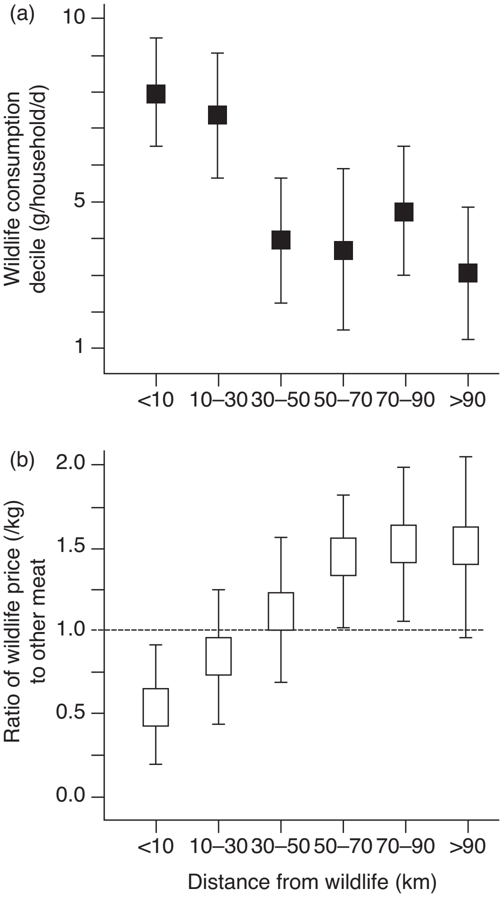

Figure 6.5 (a) Distance of human settlements from harvestable wildlife populations in Ghana, Tanzania, Madagascar and Cameroon was a strong predictor of the amount of wild meat that households in those communities consume annually as well as (b) the price that consumers paid for wild meat in Ghana and Tanzania (from Brashares et al. 2011; adapted with permission from the National Academy of Sciences, USA).

6.4.2 Non-wealth Factors

As outlined in the section above, wild meat is consumed primarily by the rural poor who live closer to wildlife areas. People eat wild meat in rural localities because it is cheaper than other meat sources or simply because no alternatives are available in the marketplace (Apaza *et al.* 2002; Wilkie & Godoy 2001). Some studies have indicated that consumers prefer the taste of wild meat (Chardonnet *et al.* 1995; Trefon & de Maret 1999) or wish to add variety to their diet and consume it for special social events and occasions (Njiforti 1996). Despite this variety of possible reasons that may motivate buyers to eat wild meat, most studies have focused on the socioeconomic background of consumers as the main reason underpinning their choice (Brashares *et al.* 2011; Wilkie & Godoy 2001). Findings relating to wealth show price and income have significant roles in determining the level of consumption of wild meat, fish, chicken and beef (Apaza *et al.* 2002; Wilkie & Godoy 2001; Wilkie *et al.* 2005). Nonetheless, as Brashares *et al.* (2011) has indicated, household wealth is only weakly associated with eating wildlife, and, thus, such a lack of a strong correlation could be explained by the undisclosed importance of other factors. Wild meat consumption can therefore be affected by other factors such as age, gender and geographical setting (Hema *et al.* 2019; Luiselli *et al.* 2017). Luiselli *et al.* (2019), using face-to-face interviews in Togo, Nigeria, Burkina Faso and Niger, examined the possible links between wild meat consumption frequency and types eaten relative to the age and gender of consumers as well as the influence of settlement type, ecological and country setting. Significant differences were evident in consumption between rural and urban areas in all four countries but the proportion of persons not consuming any wild meat was highest in urban areas. This observation was explained not by gender differences but by young people consistently avoiding wild meat, especially in urban areas. The complicated interplay between tradition and evolution of social systems (especially the trends towards Westernization) may explain the different perceptions that people have towards consuming wild meat in the four studied countries. Hence, a unifying theory of wildlife consumption will require taking into account the many drivers underlying different peoples' consumption practices, even specific to an intervention area, as suggested by Chausson *et al.* (2019). An in-depth understanding of behaviours and practices is also needed. For example, in a study of urban settlements in the Colombian Amazon, Morsello *et al.* (2015) argue that beliefs, attitudes and social norms explained consumption and preference of wild meat in the study locations. They argue that, as in Nardoto *et al.* (2011) for Amazonian towns, that even though wild meat was not the preferred source of animal protein, it was routinely consumed in the studied towns because it was the local custom.

6.5 Spatial Patterns of Extraction

Data on the spatial extraction of different species used for food can be obtained from either wild meat market studies (Fa 2007) or from records of prey taken by hunters in villages or camps (see Taylor *et al.* 2015). Most studies documenting offtake, consumption and trade of wild meat in tropical forests have focussed on West and Central Africa with much less information for South American and Asian forests (see Coad *et al.* 2019). Although the number of publications on wild meat use since the 1960s has increased significantly (see Chapter 1), most studies have targeted small catchment areas (often around single sites) over short time periods (but some regional assessments such as Fa *et al.* 2002 have been published) and limited data of wild meat extraction rates are available at a larger scale (and over longer time frames). Although such research may be affected by the lack of comparability between the studies used in the analysis, they still allow us to generate a broad understanding of wild meat extraction and availability patterns over large geographical areas. No doubt, these approximations will be further enhanced as more data becomes available. However, there is still a paucity of biological and socioeconomic data at a regional scale that can be used for determining patterns of wildlife exploitation to help decision-makers highlight areas that are at greater from unsustainable hunting (Ziegler 2010). Thus, developing regional maps delimiting hotspots of wild meat extraction can pinpoint areas requiring conservation interventions, and ultimately assist in protecting forest ecosystem and their biodiversity. Such maps are a useful data visualization tool for communicating the current situation of wildlife subjected to hunting, of use for decision-makers, protected area managers and researchers. Such maps are useful representations of the state and future of the wild meat resource and the pressures acting upon it.

A first attempt to project large-scale wild meat extraction in a large region is the spatial analyses performed in Ziegler *et al.* (2016) for Central Africa. These authors used data on the number of carcasses and species of mammals hunted in 27 sites between 1990 and 2007 in Cameroon, Central African Republic, Democratic Republic of Congo, Equatorial Guinea, Gabon and Republic of Congo. By examining the relationship between environmental and anthropogenic variables, they mapped (Fig. 6.6a) the intensity of wild meat extraction. Mean (±SD) annual total biomass offtake per recorded site was 25,657 ± 23,538 kg/yr (303–84,093 kg/yr). Catchment area sizes ranged between 45 km^2 and

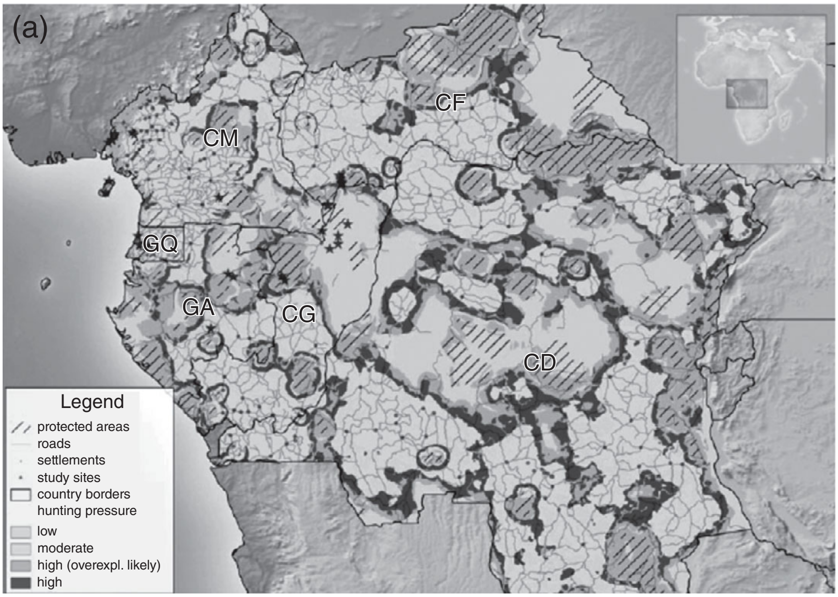

Figure 6.6 (a) Spatial prediction of hunting pressure using distance to protected areas, roads, and population density. From Ziegler *et al.* (2016) reprinted with permission from John Wiley & Sons. Risk zones: See legend for key to low, moderate, high (over exploitation likely) and high risk. CD, Democratic Republic of Congo; CG, Republic of Congo; CM, Cameroon; CF, Central African Republic; GA, Gabon; GQ, Equatorial Guinea. (b) Anthropogenic pressures (i) above median areas of rural human population density. (ii) below median areas of distance to urban areas. (iii) below median areas of distance to roads. (iv) above median areas of distance to protected areas. (v) Wild meat extraction patterns emerging from the overlay of urban areas, road networks, protected areas and densely populated rural areas (areas with a total score of 4 had the highest wild meat extraction potential, whereas areas with a total score of a 0 had the lowest). From Fa *et al.* (2015a) reprinted with permission from John Wiley & Sons.

1,010 km^2. The highest annual biomass extraction was 294 kg/km^2 but lowest recorded was 1 kg/km^2; mean annual offtake was 92 $kg/km^2 \pm 78.9$ kg/km^2. Mean (±SD) number of hunted species per site was 20 ± 8.7 (7–39 species). A number of different anthropogenic variables used to construct the map included road density and distance from the hunting locality to the nearest protected area. These proved to be adequate proxies to predict annual offtake. Lower annual offtake in areas with higher road densities explained almost 23% of the variation in annual biomass offtake per km^2 and distance from the hunting locality alone, 17%.

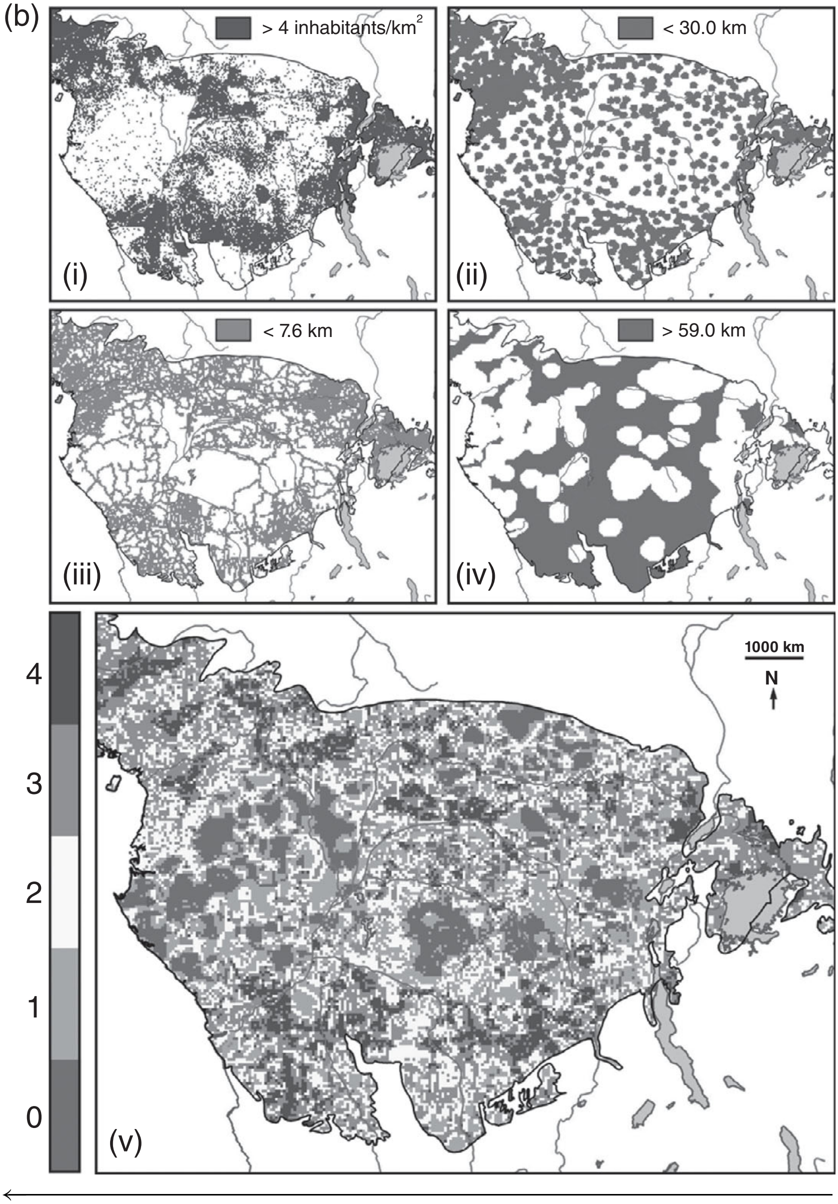

Figure 6.6 (cont.)

As expected, total annual wild meat offtake and distance to protected areas was significantly negatively correlated (Ziegler *et al.* 2016). Similarly, the number of species recorded in each site (= species richness) and road density and human population density were significantly correlated, explaining 64% of the variance. Using the median of the predicted values for annual offtake (156 kg/km^2) and hunted species (n = 16), hunting pressure was divided into four classes: (1) lower pressure (annual offtake <156 kg/km^2; number of hunted species <16), (2) moderate pressure (annual offtake >156 kg/ km^2; number of hunted species <16), (3) high pressure (annual offtake <156 kg/km^2; number of hunted species >16), and (4) very high pressure (annual offtake >156 kg/km^2; number of hunted species >16). Predicted hunting pressure areas within the study area indicated a patchy distribution (Fig. 6.6a) where many protected areas are located in predicted higher hunting pressure zones accounting for approx. 1.5 million km^2 (39%) of the total area of the Congo Basin and concentrated along three main broad zones. Approximately 36% of the Congo Basin (371,740 km^2) was characterized as zones of moderate hunting pressure, encompassing Cameroon and half of the land area of Republic of Congo and Central African Republic as well as the southern part of Democratic Republic of Congo.

Because wild meat hunters are typically central place foragers (Section 4.2), their hunting patterns should be distributed on the landscape according to how easily they can reach forested areas that support game (Levi *et al.* 2011a; Sirén *et al.* 2004). As shown in Ziegler *et al.* (2016), a well-developed infrastructure, including roads, rail- and waterways, in tropical forests, improves accessibility and transportation and therefore facilitates the extraction of wild meat in the Congo Basin. In fact, estimated hunting offtake in Ziegler *et al.* (2016) was not explained by any single environmental factor but by increased road density values and proximity to protected areas. Similar effects of road networks on hunting were found by Fuentes-Montemayor *et al.* (2009), and Benítez-López *et al.* (2019) developed a map of hunting pressure across the tropics where the distance to the nearest access point and market were used as a predictor of the spatial distribution of hunting pressure.

Simple Euclidean distance measures can successfully describe coarse patterns of game depletion even if hunting information is not considered. For example, Fa *et al.* (2015a) inferred wild meat extraction patterns using only the overlap of urban road networks, protected areas and densely populated rural areas resulting in similar patterns to the map in Zeigler *et al.* (2016) which also used hunting offtake data (Fig. 6.6b). However, according to Deith and Brodie (2020), fine-scale environmental features like topography and land cover influence hunter movement decisions while foraging and may offer more realistic and generalizable predictions of the distribution of hunting effort. These authors compared simple, commonly used measures of landscape accessibility against a novel, high-resolution accessibility model based on circuit theory and assess their ability to predict camera-trap detections of hunters across tropical forests in Malaysian Borneo. Deith and Brodie (2020) show that hunter movements are strongly correlated with the accessibility of different parts of the landscape, and these are most informative when they integrate fine-scale habitat features like topography and land cover.

Similar to extraction maps produced for the Congo Basin and Borneo, Peres *et al.* (2016) mapped the potential extent of large primate extirpation in the Brazilian Amazon. Because human hunters concentrate hunting effort near households, highly susceptible game species, such as large primates, are extirpated first near human settlements. Peres *et al.* (2016) assumed central place hunting by a single forest hunter for a total of 915,877 georeferenced rural households within different forest phytogeographic boundaries in the region. Population density, biomass density, or another abundance metric for 16 game and non-game primate species functional groups, from pygmy marmosets to the largest atelines (*Ateles* spp. and *Lagothrix* spp.) was calculated from line-transect surveys at 166 Amazonian forest sites (Fig. 6.7). This unprecedented dataset was used by the authors to determine the impact of defaunation of the most harvest-sensitive species that would lead to losses in aboveground biomass, given that primates are one of the main tree seed dispersers. The resulting map shows that areas that are heavily settled in the southern and eastern Amazon and along the main tributaries of the Amazon River are depleted (Fig. 6.8a and b), but that non-hunted refugia exist within inaccessible regions and large protected areas that are depopulated or sparsely populated. The actual spatial extent of overhunting varies regionally due to local food taboos that affect primate hunting, or the actual areas accessible to hunters; the latter may diverge due to topographic differences (see Deith & Brodie 2020). Overall, the study indicates that large primate frugivores would be completely extirpated in 103,022 km^2 and overhunted in 236,308 km^2 across Brazilian Amazonia; 3.3% and 7.5% of the total remaining forest area, respectively. The total area affected by any

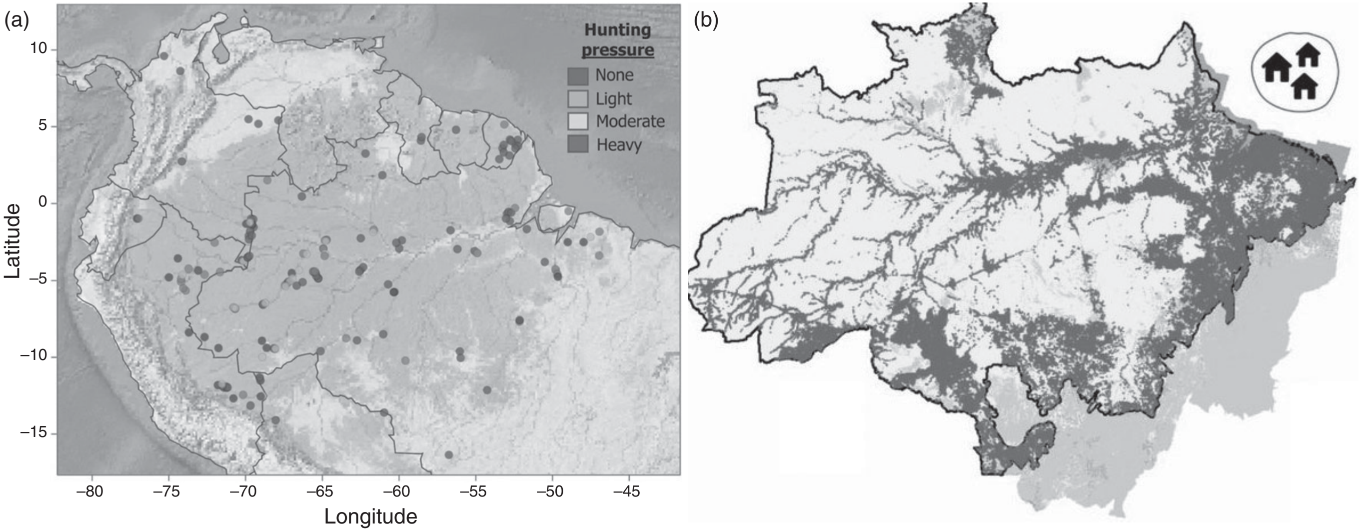

Figure 6.7 (a) Geographic location of 166 Amazonian and peri-Amazonian forest sites across eight of the nine Amazonian countries on which forest primate population density estimates were available; (b) spatial distribution of all georeferenced rural households across the phytogeographic boundaries of Brazilian Amazonia. (From Peres *et al.* 2016 reprinted with permission from the National Academy of Sciences, USA.)

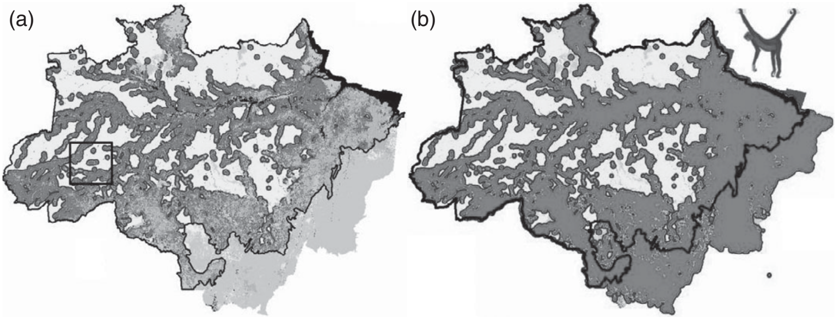

Figure 6.8 Maps (a) of the overall distribution of depletion envelopes excluding all deforested areas as of 2013 (shown in lighter grey); (b) of the population depletion envelopes for a game species that is highly sensitive to hunting (spider monkey, *Ateles* spp.) based on a biodemographic model that considers both the behaviour of central place hunters and the population dynamics of prey species. (From Peres *et al.* 2016 reprinted with permission from the National Academy of Sciences, USA.)

level of hunting represents 32.4% (1,017,569 km^2) of all remaining forest areas, approx. 1.34-times larger than the cumulative area deforested across this region over the 1970–2014 period (Peres *et al.* 2016).

The Peres *et al.* (2016) map for the Brazilian Amazon as well as Ziegler's *et al.* (2016) for the Congo Basin clearly show that there are hotspots of greater hunting pressure in those areas with more roads and with higher human population density. Similar regional assessments of hunting pressure for Southeast Asia are not available. For the Congo Basin, Ziegler *et al.* (2016) also show that the proportion of small- and medium-sized rodents in the recorded offtake studies increased significantly in areas of higher human presence. This finding is not unexpected as there is evidence that hunting pressure is likely to be higher where there are more hunters (areas of higher human population density) or where hunters have better access to hunting sites, often facilitated by more roads (Fa *et al.* 2015a). As a result, sites in less disturbed habitats will still have more intact species assemblages, with more large-bodied species present (Dupain *et al.* 2012). The higher proportion of rodents in hunter bags in African sites is an indication of a decline in slow-breeding large-bodied taxa and a replacement by faster-breeding species (see Section 5.5.3).

Differences in the composition of fauna, often related to habitat type and disturbance history, will impact the hunting potential of a region. Moreover, accessibility to hunters as well as the actual number of hunters in the region will influence the biomass of wildlife extracted. Studies of how habitat type and hunting history may explain the structure of the mammalian community in an area have been undertaken extensively for Amazonian forests (Peres 1999a, 2000). However, few studies are available for African moist forests (Effiom *et al.* 2013, 2014). As has been observed for the Amazon (Fa & Brown 2009), it is likely that type of habitat and history will affect mammalian assemblages in Africa in a similar way. In both the Amazon and the Congo Basin, environmental perturbations, such as selective logging, slash-and-burn agriculture, surface wildfires and forest fragmentation as well as hunting, can lead to marked changes in relative abundances of tropical forest vertebrates. Despite this, given the broad geographic spread in the analyses by both Peres *et al.* (2016) and Ziegler *et al.* (2016), the maps are likely to be a good reflection of the spread of hunting pressure in such large forest blocks. However, there are differences in their accuracy based on the type and quality of data used. Studies such Ziegler *et al.* (2016) employed hunting data exclusively drawn from the literature. As these data were neither random nor systematic, but determined by the contemporaneous studies that were available, the map is likely to comprise some bias. The dataset in Peres *et al.* (2016), in contrast, is drawn from field data systematically collected through line transects and, therefore, is not a reflection of game extraction but of the abundance of the game remaining. The ideal of generating data from a large sample of sites during a similar time period is not only time-consuming but also cost-prohibitive. Thus, even though literature-based or prey abundance data assessing spatial patterns of extraction may suffer some constraints (e.g. linked to the comparability of field methods and study periods, validation of study site geolocations, and determination of hunting catchment areas), results for Central Africa and the Amazon corroborate other published studies that show, as expected, higher anthropogenic activities and population densities to generate greater hunting pressure (Fa *et al.* 2015).

6.6 Estimates of Overextraction

Estimates of wild meat offtake in tropical forests range from global appraisals of what proportion wild animal protein contributes to people's diets (Prescott-Allen & Prescott-Allen 1982), to more precise extrapolations of numbers and biomass consumed within the Congo and Amazon Basins (Fa & Peres 2001; Fa *et al.* 2003). From these latter studies, extraction rates were calculated for 57 reported mammalian taxa, for a rural human population of 24 million within a forest area of 1.8 million km^2 in the Congo Basin (taken from Wilkie & Carpenter 1999). Resulting numbers suggest that as many as 579 million animals were consumed in the Congo Basin annually, producing around 4 million tonnes of dressed wild meat (Fa *et al.* 2003). This figure contrasts with Wilkie and Carpenter's (1999) study, which estimated only 1 million tonnes. The latter figure is based on extrapolations of actual meat consumed from figures assembled by Chardonnet *et al.* (1995) to estimate an average consumption of meat per person in the region. Using data on production and extraction for all mammal species exploited, Fa *et al.* (2003) calculated harvest rates from empirical data derived from hunting studies in 36 sites in seven West and Central African countries (Cameroon, Equatorial Guinea, Gabon, Republic of Congo, Democratic Republic of Congo, Central African Republic and Ghana). Although the magnitude of extraction in the two studies are different, these figures are likely to still be underestimates, since sample sizes are low. Despite this caveat, the amount of wild meat extracted and consumed per unit area in the Congo Basin is still orders of magnitude higher than in the Amazon. In terms of actual yields of dressed carcasses (given that muscle mass and edible viscera account on average for 55% of body mass), Fa and Peres (2001) estimate that 62,808 tonnes are consumed in the Amazon and around 2 million tonnes in the Congo Basin. More specifically, estimated hunting rates for Amazon and Congo Basin species, shown in a graph of production *versus* extraction (Fig. 6.9) indicate that most are exploited unsustainably in the Congo, whilst most hunted Amazonian taxa are still within the sustainable part of the graph. Congo Basin primates appear more heavily hunted than other species; 12 of the represented 17 species (>70%) fall above the 20% line.

These differences in species exploitation between the two continents are predominantly a result of larger human population sizes within a smaller forest area in the Congo Basin, and the fact that a large proportion of what hunters kill is sold in towns and villages for profit. Therefore, per capita harvest rates (kg/person/yr) in relation to number of consumers, show a lower variation for South American settlements than for Africa where they decline significantly from an average of approx. 500 kg/person/yr in smaller settlements to 1 kg/person/yr in the largest settlements (Robinson & Bennett 2004). This does not indicate greater consumption rates of wild meat per person but the fact the wild meat is commercialized.

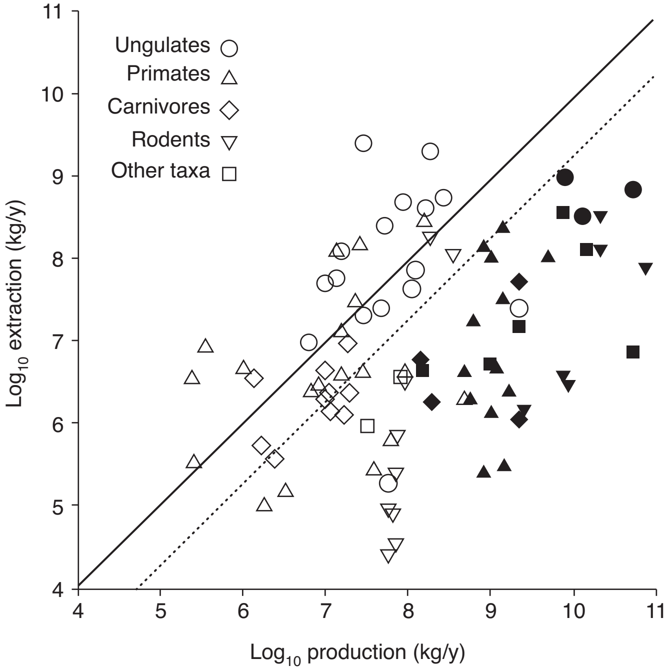

Figure 6.9 Hunting rates are unsustainably high across large tracts of tropical forests as seen in the relationship between extraction and total production of wild meat throughout the Amazon and Congo basin (solid and open symbols, respectively) by mammalian taxa. (From Fa *et al.* 2002; adapted with permission from John Wiley & Sons.)

6.7 Defaunation

The archaeological and paleontological evidence suggests that premodern peoples might have driven animal species to extinction. Mass extinction events of large-bodied vertebrates in Europe, parts of Asia, North and South America, Madagascar and several archipelagos are relatively well documented in the fossil and subfossil record (Young *et al.* 2016). Whether they are attributable to post-Pleistocene human overkill and/or climatic and environmental change remains controversial, although the latest analyses (Andermann *et al.* 2020) strongly imply that increasing human population size caused past extinctions (Box 6.1). In more recent times, extinction events induced by overexploitation have also been common as European settlers wielding superior technology expanded their territorial frontiers and introduced market and sport

Box 6.1 *Prehistoric megafaunal extinctions*

There has been a long and controversial debate on the extent of human contributions to prehistoric species extinctions, especially the late-Quaternary extinctions of megafauna. Based on different data sets, diverging assumptions and conflicting interpretations of several schools of thought have emerged:

- Humans have been driving species to extinction since the beginning of the late Pleistocene after their expansion from Africa into Europe, Asia, Australia and the Americas (Diniz-Filho 2004; Fiedel & Haynes 2004; Haynes 2007; Johnson 2002; Johnson *et al.* 2016; Klapman & Capaldi 2019; Martin & Klein 1984; Raczka *et al.* 2019; Sandom *et al.* 2014; Smith *et al.* 2018; Surovell *et al.* 2005, 2016). Key is a strong human hunting pressure leading to overkill, particularly of megafauna mammals (Whittington & Dyke 1984); blitzkrieg, that is rapid overkill (Mosimann & Martin 1975); and a sitzkrieg, that is hunting alongside habitat fragmentation, fire and introduction of exotic species and diseases (Diamond 1989).
- Others have argued that there is insufficient evidence for hunting as the cause of human-caused extinctions or that extinction models are highly sensitive to underpinning assumptions about the extinction dynamics (Grayson & Meltzer 2003, 2004; Lima-Ribeiro *et al.* 2013; Lima-Ribeiro & Diniz-Filho 2017). On the other hand, Emery-Wetherell (2017) highlights that maps of last megafaunal occurrence in North America are consistent with climate as a primary driver in some areas, but the analysis cannot reject human activities as contributing causation in all regions.
- Some argue that rapid or synchronous continental-wide extinction is not human-mediated but extinctions are associated with sustained climatic and environmental change especially due to glacial-interglacial cycles during the late Quaternary (Hocknull *et al.* 2020; Lorenzen *et al.* 2011; Wroe & Field 2006; Wroe *et al.* 2004).
- Some data indicate situation-specific extinction dynamics with differing underpinning causations whereby the importance of hunting and other factors such as climatic and environmental change varied considerably between sites and continents (Wroe *et al.* 2004). For example, Broughton and Weitzel (2018) concluded that the causes for extinctions in North America varied across taxa and by region whereby either extinctions are linked to hunting (mammoth,

horse, sabre-toothed cat); to climate and ecological change (Shasta ground sloth, mastodon, mammoth in the Great Lakes region); or to both (mammoth in the Southwest region).

- A synthetic model ascribes extinctions to the combined effect of humans and climate change (Barnosky 2004; Bartlett *et al.* 2016; Gibbons 2004; Haynes 2018; Mondanaro *et al.* 2019; Prescott *et al.* 2012; Saltré *et al.* 2019).
- In a study applying Bayesian models to the fossil record to estimate how mammalian extinction rates have changed over the past 126,000 years, Andermann *et al.* (2020) showed that human population size is able to predict past extinctions with 96% accuracy. This study combined data of prehistoric extinctions of 271 mammal species since the beginning of the late Pleistocene and 80 mammal extinctions since the year 1500. Predictors based on past climate, in contrast, perform no better than expected by chance, suggesting that climate had a negligible impact on global mammal extinctions.

hunting. A prime example is the catastrophic loss of wildlife driven by uncontrolled market hunting, and unrelenting subsistence killing suffered in North America at the end of the nineteenth century (Mahoney & Geist 2019). Such unbridled hunting for meat, skins or merely recreation led to near extinction of once-vast bison herds in North America. There is also the notorious example of the extinction of what was once the most numerous bird in the world, the passenger pigeon (Bucher 1992).

Highly visible anthropogenic threats, such as deforestation, habitat degradation and climate change, have been the focus of much of our attention on biodiversity loss, often overshadowing the effects of direct exploitation. But overhunting is at least as serious a problem, often resulting in environments that might appear to be pristine but are devoid of wildlife, especially large-bodied wildlife (Peres *et al.* 2006). The meta-analysis of 176 hunting studies by Benítez-López *et al.* (2017) revealed that bird and mammal abundances were 58% (25% to 76%) and 83% (72% to 90%) smaller in hunted compared with unhunted areas. Abundances were reduced within 7 and 40 km from roads and settlements for birds and mammals, respectively. The commercial aspect of defaunation was evident by the fact that accessibility to major towns where wild meat could be traded impacted depletion.

Remote sensing data have indicated that only 23.5% of the current extent of forest ecosystems was considered intact in 2008, defined as containing an unbroken expanse of natural ecosystems within areas of current forest extent, without signs of significant human activity (Potapov *et al.* 2008). However, whilst remote sensing can identify habitat loss, conversion and degradation, it does not account for 'empty forests' (sensu Redford 1992) due to hunting. Benítez-López *et al.* (2019) mapped the spatial patterns of mammal defaunation in the tropics in what appear intact forests using a database of 3,281 mammal abundance declines from local hunting studies. They found an average abundance decline of 13% across all tropical mammal species, but there were large differences regarding mammals of different body size (Fig. 6.10). Medium-sized species were being reduced by >27% and large mammals by >40%. Defaunation, defined here as declines of 10% or more (see Section 6.7.1), was predicted on half of the pantropical forest area, 52% of the intact forests, 62% of the wilderness areas and 20% of protected areas in the tropics, particularly in West and Central Africa and Southeast Asia.

As an example, unprecedented rates of local extinctions of medium to large-bodied mammals have been demonstrated from the Atlantic Forest biome in eastern South America. This biome is one of the world's most important tropical biodiversity hotspots and one of the 'hottest' of the global biodiversity hotspots (Myers *et al.* 2000). Only 10.8% of the original forest cover in the surveyed four biogeographic subregions has been converted to other land-uses (Ribeiro *et al.* 2009). What remains of the original forest has only 767 from a possible 3,528 populations of ten terrestrial and seven arboreal mid- to large-bodied mammal species still persisting (Canale *et al.* 2012). Patchiness of remaining forest fragments makes populations especially vulnerable as fragments are highly accessible to hunters. Forest patches retained only 3.9 out of 18 potential species occupancies on average. Geographic ranges had contracted to 0–14.4% of their former distributions. In the Atlantic rainforest's Serra do Mar bioregion, mammalian biomass declined by up to 98% in intensively hunted sites (Galetti *et al.* 2017). This level of overkill was also confirmed by using the fate of selected surrogate Neotropical large mammal species to map the level of defaunation. Jorge *et al.* 2013) mapped the occurrence of the jaguar, tapir, white-lipped peccary and the muriqui – the largest apex predator, herbivore, seed predator and arboreal seed disperser, respectively – in 94 locations of Atlantic Forest remnants. They observed that 96% of these sites are depleted of at least one of the four surrogate species and 88% are completely depleted of all four surrogate species.

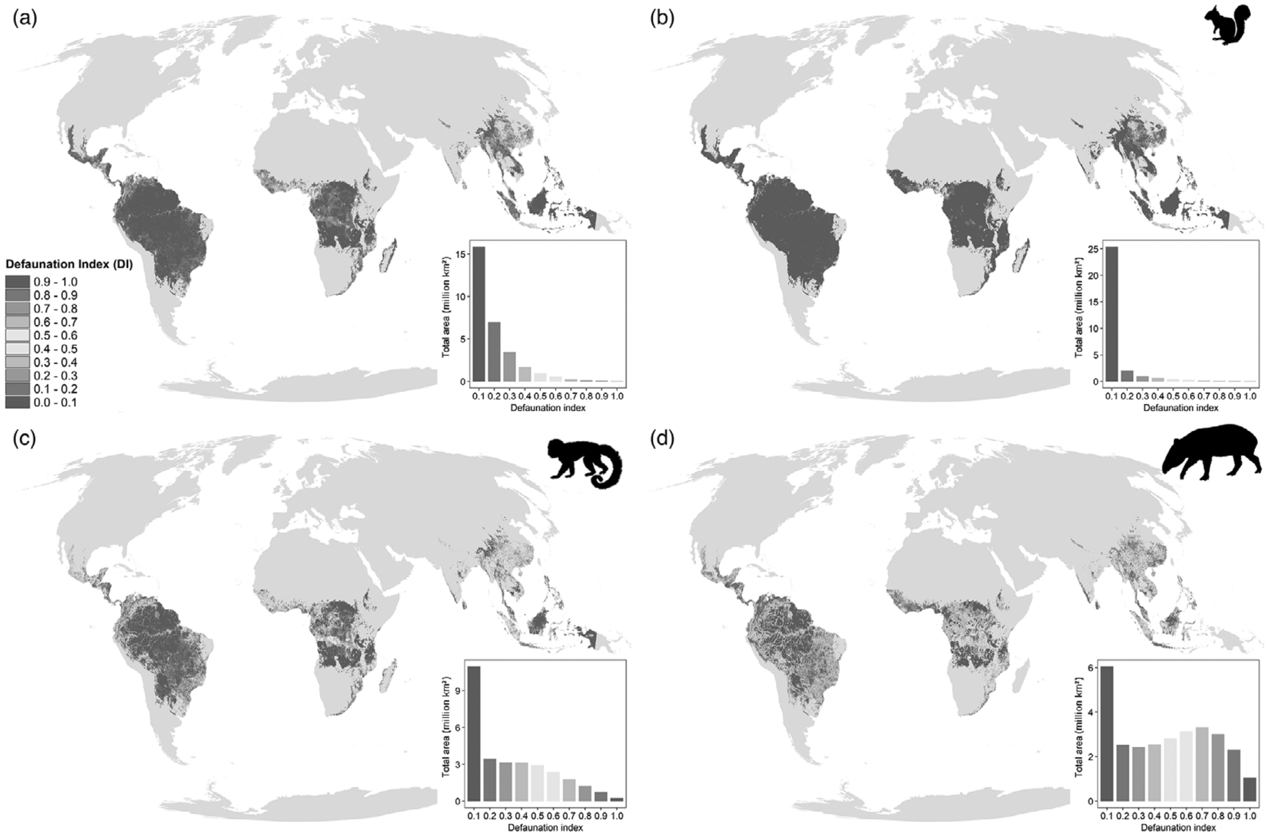

Figure 6.10 Geographic variation in hunting-induced defaunation for (a) all species, (b) small-sized species (<1 kg, e.g. *Sciurus* spp.), (c) medium-sized species (1–20 kg, e.g. *Alouatta* spp.), and (d) large-sized species (>20 kg, e.g. *Tapirus* spp.). The insets represent the total area (*y*-axis) under different levels of defaunation (*x*-axis, from D = 0 to D = 1). Note that the *y*-axes in the four insets have different scales. (From Benítez-López *et al.* 2019; adapted with permission from PLOS Biology.)

6.7.1 Defaunation Index

The defaunation index (DI) of Giacomini and Galetti (2013) quantifies the loss of species richness through matched site comparisons between an affected contemporary site and a reference site which represents a non-affected contemporary or historic site (e.g. in a forest fragment and a nearby protected area as a reference site). The index ranges from 0.0 for a completely intact faunal assemblage in the study area to 1.0 for a completely defaunated study site to −1.0 for a completely defaunated reference site. A defaunated reference site may seem counterintuitive as the reference site is supposed to be non-affected by species loss but negative DI values might arise due to species reintroductions or invasive species in the affected site. The index can be applied to different types of data – species occurrence, biomass, or site occupancy –depending on practical limitations and data availability.

It is the only index that allows quantification of the effects of hunting on the reduction of species richness in a given area. Even when a contemporary reference site is not available, probable occurrences can be estimated using known distribution maps for species assessed by the Red List (IUCN 2020b). Although these range maps are estimated themselves based on often limited available information, the use of the IUCN polygons is a widely established methodology (Bogoni *et al.* 2018). The index can be geared towards the importance of species for different biological aspects, such as ecosystem function or conservation importance by the weight parameter for species importance that is part of the equation to calculate DI.

The index quantifies species loss for any reason and cannot distinguish whether the loss occurred because of hunting, habitat alteration, habitat fragmentation or the non-synergistic or synergistic combination of these. Moreover, the index is unsuited for the practical assessment of sustainability of hunting for management purposes as it is an a posteriori assessment of species loss that has already occurred rather than a method that can flag-up non-sustainable hunting whilst the target species still occur and intervention is still possible. Depending on the choice of the weight parameter, different DI values might be calculated for the same data set; thus, DI values are not always directly comparable between studies and sites. For example, species importance might be equal for any species, resulting in DI values that follow an exact monotonically decreasing function of richness. If, however, species' body size is taken as weight to act as a proxy for vulnerability to extinction and conservation concern, the resulting DI values can vary substantially at the same richness. Other choices for the assumed weight are possible. Giacomini and Galetti (2013) point out that the criteria for its choice must be justified on a priori grounds and not on a posteriori inspection of resulting index values.

Example: Bogoni *et al.* (2018) calculated the DI for the entire mammal assemblage and for functional groups within the Atlantic Forest of South America which is one of the most endangered major ecoregions worldwide. Because only 11.7% of its original vegetation cover remains and the remaining habitat fragments are mostly highly disturbed (Ribeiro *et al.* 2009), historic species assemblages were reconstructed from the probable species occurrences calculated from the Red List geographic range polygons. A total of 105 studies provided data on 497 mammal assemblages from 164 independent clusters of study sites from which mammal inventories are available. The results showed high levels of defaunation of DI $>$ 0.5 for most of the Atlantic forest. Comparing contemporary and historical mammal assemblages at any given site for all mammal taxa yielded a mean total defaunation index of 0.71 ± 0.25 ranging from 0.61 for small-bodied species to 0.76 for large-bodies species and to 0.79 for apex-predators (Fig. 6.11). Accounting for possible overestimation of the historical baseline through existing mammal distribution polygons, smaller but still very large DI values were estimated with a mean overall index of 0.57 ± 0.20. The geographic distribution of DI values across the entire Atlantic Forest biome was interpolated from the geographic distribution of the DI values in the separate clusters of study sites by kriging which accounts for spatial autocorrelation of the data. The eastern portions of the Atlantic Forest contain the regions with the highest levels of defaunation (see Bogoni *et al.* 2018, fig. 4).

6.7.2 Ecological Consequences of Defaunation

Defaunation not only has the above-described devastating effects on the species involved, but also on a plenitude of cascading effects that result in changed and depauperated environments, ecosystem services and human food security. Defaunation has long-term cascading effects on animal and plant community structure and ecosystem functioning, which manifests in a myriad way.

In predator–prey systems, prey species benefit from the removal of their predators, which can trigger further effects on various ecosystem

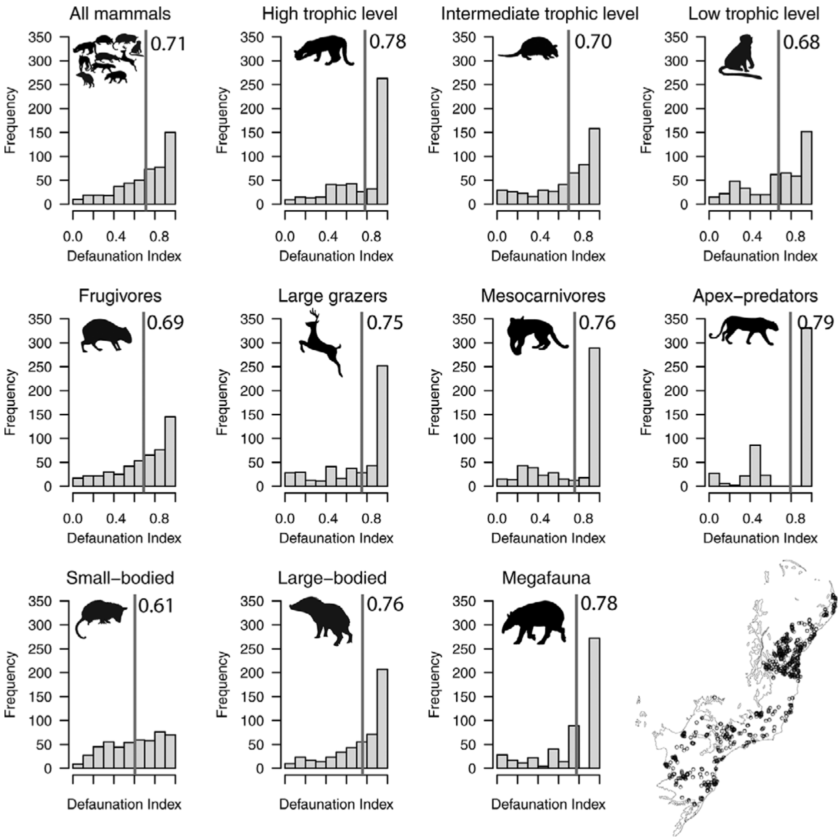

Figure 6.11 Frequency distribution of the overall defaunation index for medium- to large-bodied mammals across the Atlantic Forest biome of South America. The heavy vertical lines indicate mean values. Inset map (lower right) shows the geographic distribution of study sites in eastern Brazil. (From Bogoni *et al.* 2018; reprinted with permission from PLOS ONE.)

services. For example, sea otters on the northern Pacific coast of North America are sensitive to overhunting and became almost extinct in the nineteenth and twentieth centuries (Estes 1990). Sea otters prey on sea urchins, which in turn feed on kelp. Wilmers *et al.* (2012) calculated that kelp net primary productivity is 25–70 g C/m^2/year in the absence of otters, but over 10-fold higher when they are present (313–900 g C/m^2/year). The ecosystem service by increase in carbon storage is estimated to be worth US\$205 million to \$408 million on the European Carbon Exchange for the otter's ecosystem area of approximately 5.1 × 10^{10} m^2.

Another reduced ecosystem service by defaunation involves changes to prevalence and transmission of some zoonotic disease (Chapter 7). Young *et al.* (2014) experimentally excluded large wildlife from a savanna ecosystem in East Africa. Consequently, rodent population density doubled and with it the density their flea vectors infected with *Bartonella* spp., which causes bartonellosis in humans. Similar cascading effects by reductions in predator abundance increase the zoonotic risk of hantavirus and Lyme disease (Levi *et al.* 2012; Suzán *et al.* 2009). Human welfare is also impacted by ecosystem services such as the suppression of pest insects and, to a lesser extent, pollination services by birds and bats. Maas *et al.* (2013) observed in their exclusion experiments in Indonesian cacao agroforestry fields that insect herbivore abundance increased leading to the decrease of 31% of crop yield in this billion dollar per year industry.

A growing body of studies has demonstrated a significant impact of the defaunation of mid- and large-sized animals on plant regeneration and thus carbon storage through changes in seed dispersal, pre- and post-dispersal seed predation, leaf herbivory or browsing. Exclusion experiments have demonstrated increased seedling density, survival, recruitment and increased understory vegetation cover through reduced seed predation and herbivory (Aliaga-Rossel & Fragoso 2014; Beck *et al.* 2013). Whilst such experiments can demonstrate that plant community structure depends on vertebrate community structure, they are no analogues for real-world defaunation because they impact vertebrate communities differently. Exclusion experiments also exclude herbivores (e.g. ungulates) or seed predators (e.g. rodents), which are not hunted or hunted but not critically depressed in their abundance in real-world settings. Moreover, they fail to exclude arboreal and volant species such as primates, birds and bats, many of which are seed dispersers. Contrary results were observed by Rosin and Poulsen (2016) in experiments that excluded large animals but not rodents. Here, rodents caused the greatest seed mortality for all species, removing 60% of accessible seeds, leading to a reduction of seedling establishment by 42% compared to sites with intact fauna. Gardner *et al.* (2019) conducted a meta-analysis of real-world defaunation and manipulation experiments and confirmed these contrasting findings. Observed defaunation was associated with reduced forest regeneration whilst experiments were associated with increased forest regeneration. Overall, defaunation caused decreases in seedling density and richness. The defaunation of primates and birds caused the greatest declines in forest regeneration.

Defaunation changes the spatial structure and dynamics of tree populations and leads to a decline in local tree diversity over time (Harrison *et al.* 2013) because hunting directly impacts tree species whose seeds are dispersed by animals. For example, defaunation causes population genetic changes in the large-seeded queen palm in the Atlantic Forest of South America whereby trees in hunted forest fragments show lower allelic richness and stronger fine-scale spatial genetic structure compared to protected forest (Giombini *et al.* 2017). In a meta-analysis, Kurten (2013) confirmed that larger-seeded species consistently experience reduced primary seed dispersal when large seed-dispersing animals are absent. Resilient frugivores, such as small birds, bats and marsupials, which are not targeted by hunters, can disperse seeds up to 12.0 ± 1.1 mm in width, but larger animal-dispersed seeds are dispersed only by larger animals (Bello *et al.* 2015). Moreover, there is a functional relationship between seed diameter and traits related to carbon storage, with trees that produce seeds larger than 12 mm having a high carbon stock capacity. Thus, large seed dispersers are functionally linked to forest carbon storage (Bello *et al.* 2015). Consequently, overhunting of larger seed-dispersing animal species shifts plant species composition towards species, including lianas and low wood-density tree species, that are abiotically dispersed or dispersed by small animals(Kurten *et al.* 2015). Defaunation can negatively impact carbon storage in tropical forests by favouring the latter species as they store much less carbon than high wood density trees, which have typically large seed size (Bello *et al.* 2015; Jansen *et al.* 2010; Putz 1983). There is a relationship between wood volume and seed size with large-seeded animal-dispersed trees being larger than small-seeded animal-dispersed species, but smaller than abiotically dispersed species (Osuri *et al.* 2016). Because defaunation impacts preferentially large-bodied animal species, which disperse large seeds and, thus, large trees, defaunation shifts tree populations towards species with smaller trees. Consistent with this are simulations which demonstrate that African, American and South Asian forests, which have high proportions of animal-dispersed species, consistently show carbon losses (2–12%) when becoming defaunated, whereas Southeast Asian and Australian forests, where there are more abiotically dispersed species, show little to no carbon losses (Osuri *et al.* 2016). Field studies in Africa (Effiom *et al.* 2013, 2014; Poulsen *et al.* 2013; Vanthomme *et al.* 2010), Mesoamerica (Kurten *et al.* 2015; Wright *et al.* 2007), southern Asia (Brodie *et al.* 2009) and Southeast Asia (Chanthorn *et al.* 2019) corroborate that defaunation of large frugivore, seed-dispersing species affects the recruitment, relative abundance and population growth rate of animal-dispersed large-seeded trees. Loss of dispersal is also substantiated by the increase of genetic similarity in tree communities due to defaunation (Pérez-Méndez *et al.* 2016). In an Afrotropical forest, hunting reduced the mean dispersal distances of nine mammal-dispersed tree species by 22% (Poulsen *et al.* 2013). Hunted forest also had significantly lower above-ground biomass than logged and undisturbed forests. Using field data and models to project the impact of hunting on large primates in the Brazilian Amazon, Peres *et al.* (2016) found that loss of large primates alone leads to losses in aboveground biomass of 2.5–5.8% on average, with some losses as high as 26.5–37.8%. Such changes in plant structure, dynamics, regeneration, etc., affect the forest's ability to store carbon which impacts us globally.