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BIODIVERSITY AND ECOSYSTEM SERVICES IN TROPICAL FORESTS: THE ROLE OF FOREST ALLOCATIONS IN THE DJA AREA, CAMEROON

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Abstract

Due to human-driven environmental changes, planet Earth has entered the new Anthropocene era, with major impact on biological diversity recognized as the sixth mass extinction period. The concepts of biodiversity and ecosystem services (ES) have risen to objectify and measure the human impacts on ecosystems and the many-fold contributions of ecosystems to human well-being. Among global terrestrial ecosystems, tropical forests are particularly important for the conservation of biodiversity and for the provision of ES. Agricultural conversion, logging, hunting, commercial poaching and over-harvesting lead to deforestation, degradation and defaunation of tropical forests, with highly variable consequences depending on many local factors. In Central Africa in particular, biodiversity and ES have been far less studied than in other tropical regions, despite the vital roles of these tropical forests in the livelihood of tens of millions of people in a context of high poverty. A better understanding of the determinants of biodiversity and ES in Central Africa is crucial for improving human well-being and the resilience of forest ecosystems. Despite the still relatively preserved tree cover across the region, biodiversity and ES may differ depending on forest land management and allocations. Therefore, the objective of this thesis is to assess the conservation value of tropical forests in southeastern Cameroon, as well as the supply of ES and use by local populations, in three contrasted forest allocations: a protected area, a Forest Stewardship Council (FSC)-certified logging concession, and three community forests.

First, we assessed the conservation value of the three forest allocations, examining species richness and composition of two taxonomic groups: mammals inventoried with 44 camera traps, and dung beetles inventoried with 72 pitfall traps (**Chapter 2**). We also aimed to identify the determinants of forest conservation value, disentangling the effects of forest allocations, proximity to human settlements (villages and roads), and local forest habitat. Mammal and dung beetle species showed lower species richness in the community forests than in the protected area, and intermediate values in the logging concession. Proximity to human settlements and disturbance was negatively correlated to species richness of both groups, negatively correlated with species body size, and associated to the loss of the most threatened mammal species. The high species variability among forest allocations (*i.e.*, spatial turnover) suggests that any conservation initiative should integrate many sites to protect a multitude of species, and not only large isolated areas. The high conservation value of the protected area has been confirmed, and the logging concession can play a complementary role in conservation strategies through landscape connectivity. In contrast, community forests are particularly defaunated due to their proximity to roads and villages, but they still provide wild proteins to local populations.

Second, we assessed the perceptions of the supply of ES by tropical forests to local populations, and the determinants of these perceptions (**Chapter 3**). We evaluated

the significance and abundance of ES by conducting a questionnaire survey with 225 forest stakeholders. The most significant ES perceptions were provisioning services (93% of respondents) and cultural services (68%), while regulating services were much less reported (16%). The perceptions of ES abundance were relatively homogeneous among forest allocations and respondents. Bushmeat provision has been identified as the only significant ES for local populations that is not supplied in high abundance.

Third, we depicted the use of ES by local populations in three villages, and we evaluated its determinants and sustainability (**Chapter 4**). We used diverse interviews and field surveys to assess three provisioning services (bushmeat, firewood, and timber) and five cultural services (cultural heritage, inspiration, spiritual experience, recreation, and education). On average, local populations consumed 56 kg of bushmeat person^{-1} year^{-1} (hunting zones covering on average 213 km^2 per village), 1.17 m^3 of firewood person^{-1} year^{-1} (collection zones on average 4 km^2 per village), and 0.03 m^3 of timber person^{-1} year^{-1}. On average, 59% of respondents recognized the importance of cultural services. The main determinants of ES use were forest allocations, population size, and deforestation rate, and we also showed slight differences between Baka and Bantu people in the use of cultural services. Firewood and timber have been shown to be used sustainably by local populations in this area, whereas bushmeat hunting and consumption have exceeded sustainability thresholds.

Finally, the main findings of the thesis are summarized and their practical implications are discussed, in particular for the role of forest allocations (**Chapter 5**). The potential reconciliation between conservation and the sustainable use of tropical forests is discussed. Methodological feedbacks are given for the use of mammals and dung beetles as biodiversity indicators. Research perspectives are presented for a better understanding of the interactions between biodiversity and ES. Finally, different perspectives for integrating the concept of ES in tropical forest management are given: for instance, identifying and resolving conflicts among stakeholders, raising awareness, making decisions, or evaluating the effectiveness of conservation measures. In particular, ES are increasingly used in concrete management applications, such as FSC-certification, payments for environmental services, UNESCO Man and Biosphere Reserves, and various development projects.

En raison des changements environnementaux provoqués par l'homme, la planète Terre est entrée dans la nouvelle ère de l'Anthropocène, avec un impact majeur sur la diversité biologique, reconnu comme la sixième période d'extinction massive. Les concepts de biodiversité et de services écosystémiques (SE) ont émergé pour objectiver et mesurer les impacts de l'homme sur les écosystèmes, ainsi que les multiples contributions des écosystèmes au bien-être humain. Parmi les écosystèmes terrestres mondiaux, les forêts tropicales sont particulièrement importantes pour la conservation de la biodiversité et pour l'approvisionnement en SE. La conversion agricole, l'exploitation forestière, la chasse, le braconnage commercial et la surexploitation des ressources entraînent la déforestation, la dégradation et la défaunation des forêts tropicales, avec des conséquences très variables en fonction de nombreux facteurs locaux. En Afrique centrale en particulier, la biodiversité et les SE ont été beaucoup moins étudiées que dans les autres régions tropicales, malgré le rôle vital de ces forêts tropicales dans les moyens de subsistance de dizaines de millions de personnes dans un contexte de grande pauvreté. Il est crucial de mieux comprendre les facteurs influençant la biodiversité et les SE en Afrique centrale pour améliorer le bien-être humain et la résilience des écosystèmes forestiers. Malgré le couvert forestier encore relativement préservé dans la région, la biodiversité et les SE peuvent différer selon la gestion et les affectations des terres forestières. Par conséquent, l'objectif de cette thèse est d'évaluer la valeur de conservation des forêts tropicales dans le sud-est du Cameroun, ainsi que la fourniture de SE et leur utilisation par les populations locales, dans trois affectations forestières contrastées : une aire protégée, une concession forestière certifiée par le *Forest Stewardship Council* (FSC), et trois forêts communautaires.

Tout d'abord, nous avons évalué la valeur de conservation des trois affectations forestières, en examinant la richesse et la composition spécifique de deux groupes taxonomiques : les mammifères inventoriés avec 44 pièges photographiques, et les coléoptères coprophages (bousiers) inventoriés avec 72 pièges à fosse (**Chapitre 2**). Nous avons également cherché à identifier les facteurs déterminants de la valeur de conservation des forêts, en démêlant les effets des affectations forestières, de la proximité aux villages et aux routes, et de l'habitat forestier local. Les espèces de mammifères et de bousiers ont montré une richesse spécifique plus faible dans les forêts communautaires que dans l'aire protégée, et des valeurs intermédiaires dans la concession forestière certifiée FSC. La proximité aux villages et aux routes, ainsi que les perturbations humaines étaient négativement corrélées à la richesse en espèces des deux groupes, corrélées négativement à la masse corporelle des espèces et associées à la perte des espèces de mammifères les plus menacées. La grande variabilité en espèces entre les affectations forestières (*i.e.*, *turnover*) suggère que toute initiative de conservation devrait intégrer de nombreux sites pour protéger une multitude d'espèces, et pas seulement de grandes zones isolées. La grande valeur

conservatoire de l’aire protégée a été confirmée et grâce à la connectivité paysagère, la concession forestière peut contribuer de manière complémentaire aux stratégies de conservation. Par contre, les forêts communautaires montrent une défaunation importante due à leur proximité aux routes et villages, mais elles continuent pourtant à fournir des protéines animales aux populations locales.

Deuxièmement, nous avons évalué les perceptions de l'offre en SE par les forêts tropicales aux populations locales, et les facteurs déterminants de ces perceptions (**Chapitre 3**). Nous avons évalué l'importance et l'abondance des SE en menant une enquête par questionnaire auprès de 225 acteurs du secteur forestier. Les perceptions des plus importants SE comprenaient les services d'approvisionnement (93% des répondants) et les services culturels (68%), tandis que les services de régulation étaient beaucoup moins signalés (16%). Les perceptions de l'abondance des SE étaient relativement homogènes parmi les affectations forestières et les répondants. L'approvisionnement en viande de brousse pour les populations locales a été identifié comme le seul SE important qui n'est pas fourni abondamment.

Troisièmement, nous avons décrit l'utilisation des SE par les populations locales dans trois villages, et nous avons évalué ses facteurs déterminants et sa durabilité (**Chapitre 4**). Nous avons mené divers entretiens et enquêtes de terrain pour évaluer trois services d'approvisionnement (viande de brousse, bois de feu et bois d'œuvre) et cinq services culturels (patrimoine culturel, inspiration, expérience spirituelle, détente, et éducation). En moyenne, les populations locales ont consommé 56 kg de viande de brousse personne^{-1} an^{-1} (zones de chasse couvrant en moyenne 213 km² par village), 1,17 m³ de bois de chauffage personne^{-1} an^{-1} (zones de collecte en moyenne de 4 km² par village), et 0,03 m³ de bois personne^{-1} an^{-1}. En moyenne, 59% des personnes interrogées ont mentionné l'importance des services culturels. Les principaux facteurs déterminants de l'utilisation des SE étaient les affectations forestières, la taille de la population et le taux de déforestation, et nous avons également montré de légères différences entre les Baka et les Bantous dans l'utilisation des services culturels. Il a été démontré que le bois de feu et le bois d'œuvre sont utilisés de manière durable par les populations locales dans cette région, tandis que la chasse et la consommation de viande de brousse ont dépassé les seuils de durabilité.

La conclusion générale (**Chapitre 5**) résume les principaux résultats de la thèse et discute leurs implications pratiques, en particulier concernant le rôle des affectations des terres. La réconciliation potentielle entre la conservation et l'utilisation durable des forêts tropicales est discutée. Des retours méthodologiques sont donnés sur l'utilisation des mammifères et des bousiers comme indicateurs de biodiversité. Des perspectives de recherche sont présentées pour une meilleure compréhension des interactions entre la biodiversité et les SE. Enfin, différentes perspectives d'intégration du concept de SE sont données pour la gestion des forêts tropicales : par exemple, l'identification et la résolution des conflits entre les parties prenantes, la sensibilisation, la prise de décisions ou l'évaluation de l'efficacité des mesures de conservation. En particulier, les SE sont de plus en plus utilisées dans des applications concrètes de gestion, telles que la certification FSC, les paiements pour services environnementaux, les réserves de l'UNESCO pour l'homme et la biosphère, et divers projets de développement.

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Chapter 2: Conservation value of forest allocations

Chapter 3: Perceptions of ecosystem services supplied by tropical forests to local populations

Chapter 4: Use of forest ecosystem services by local populations

Chapter 5: General conclusion

CICES:	Common International Classification of Ecosystem Services
CF:	Community forests
DPSIR:	Drivers-Pressures-Status-Impacts-Responses
EBM-DPSER:	Driver, Pressure, State, Ecosystem service, and Response
ECOFAC:	*Programme de conservation et de valorisation des Ecosystèmes Fragilisés d'Afrique Centrale*
ES:	Ecosystem services
ESP:	Ecosystem service provider
EVAMAB:	Economic valuation of ecosystem services in Man and Biosphere Reserves
FAO:	Food and Agriculture Organization of the United Nations
FCFA:	*Franc CFA*
FESP:	Framework for Ecosystem Service Provision
FRMi:	*Forêt Ressources Management Ingénierie*
FSC:	Forest Stewardship Council
GDP:	Gross Domestic Product
GIZ:	*Deutsche Gesellschaft für Internationale Zusammenarbeit*
GMDC:	The Grande Mayumba Development Company
GPS:	Global Positioning System
InVEST:	Integrated Valuation of Ecosystem Services and Tradeoffs
IPBES:	Intergovernmental Platform on Biodiversity and Ecosystem Services
IUCN:	International Union for Conservation of Nature
NA:	Missing data
NCP:	Nature's Contributions to People
NFE:	National Forest Estate (in Cameroon)
NMDS:	Nonmetric Multidimensional Scaling
n.s.:	Not significant
NTFP:	Non-timber forest products
PEFC:	Programme for the Endorsement of Forest Certification
REDD+:	Reducing Emissions from Deforestation and Forest Degradation
sPLS:	Sparse Partial Least Squares method
SWOT:	Strengths, Weaknesses, Opportunities, and Threats
TEAM:	Tropical Ecology, Assessment and Monitoring Network
TEEB:	The Economics of Ecosystems and Biodiversity
UNESCO:	United Nations Educational, Scientific and Cultural Organisation
VIP:	Variable Importance in the Projection (obtained from sPLS)

1

General introduction

1. Ecosystems in the Anthropocene

1.1. Major changes at global scale

Human activities have transformed and altered Earth's ecosystems in many ways: major land transformations, alterations of marine ecosystems, increase of carbon dioxide concentration in the atmosphere, alterations of the biogeochemical cycles, and biotic changes, among others (Vitousek *et al.*, 1997). The global environmental changes induced by human activities are so profound that a new era called the Anthropocene has been defined (Lewis and Maslin, 2015). Meanwhile, the current trends of species declines and extinctions, also induced by human activities, are qualified as the Earth's sixth mass extinction (*e.g.*, Ceballos *et al.*, 2015). Among terrestrial vertebrates, even the 'least concerned' species show dramatic and rapid population loss (Ceballos *et al.*, 2017). This global biological annihilation has detrimental cascading consequences on ecosystems, their resilience to environmental changes, and the services provided to human populations (Chapin *et al.*, 2000). In this context, the concepts of 'biodiversity' and 'ecosystem services' (ES) are particularly important for understanding how environmental changes directly impact the goods and services provided by ecosystems and contributing to human well-being (Chapin *et al.*, 2000).

1.2. Biodiversity

'Biodiversity', the contraction of 'biological diversity', is defined as 'the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems' (United Nations, 1992). Biodiversity supports the functioning of ecosystems, 'ecosystem' being defined as 'a dynamic complex of plant, animal and micro-organism communities and the non-living environment interacting as a functional unit' (United Nations, 1992). Throughout this thesis, the expression 'conservation value' is also used to refer to the role and potential of a delimited area to conserve biodiversity, which can be approximated through the inventory of specific taxonomic groups, considered or demonstrated to be representative indicators of biodiversity (Stork *et al.*, 2017).

1.3. Ecosystem services

Ecosystem services constitute the 'contributions of ecosystems to human well-being' (Burkhard *et al.*, 2012). The concept was first defined in the late 1970's (Ehrlich and Ehrlich, 1981; Westman, 1977) and has been much larger popularized by the Millennium Ecosystem Assessment (2005). ES have been used in a variety of methodological frameworks: the Integrated Valuation of Ecosystem Services and Tradeoffs – InVEST (Daily *et al.*, 2009), the Framework for Ecosystem Service Provision – FESP (Rounsevell *et al.*, 2010), the Press-Pulse Dynamics (Collins *et* *al.*, 2010), The Economics of Ecosystems and Biodiversity – TEEB (R. S. de Groot *et al.*, 2010), the Drivers-Pressures-Status-Impacts-Responses – DPSIR (Pinto *et al.*, 2013), the Driver, Pressure, State, Ecosystem service, and Response – EBM-DPSER (Kelble *et al.*, 2013), or the Common International Classification of Ecosystem Services (CICES, 2018), among others. A new conceptual framework has been developed by the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), building on the concept of 'nature's contributions to people' or NCP (Díaz *et al.*, 2018; Pascual *et al.*, 2017), highlighting the importance of culture, indigenous and local knowledge. This sparked an intense debate in the ES community on the relevance to shift to new concepts as ES only began to be integrated in the decision-making processes[1]. Despite this debate, all agree that ES constitute the link between ecosystems and humans, with a distinction between the supply of ES (amount of ES provided by ecosystems), and the use of ES (amount of ES operated by humans). In addition, ES are classically divided into three categories: provisioning, regulating, and cultural services (R.S. de Groot *et al.*, 2010). Provisioning services encompass 'all nutritional, non-nutritional material and energetic outputs from living systems as well as abiotic outputs' (CICES, 2018). Regulating services correspond to 'all the ways in which living organisms can mediate or moderate the ambient environment that affects human health, safety or comfort, together with abiotic equivalents' (CICES, 2018). Cultural services relate to 'all the non-material, and normally non-rival and non-consumptive, outputs of ecosystems (biotic and abiotic) that affect physical and mental states of people' (CICES, 2018).

Several techniques are described for assessing ES and obviously, it is extremely difficult to provide a complete integrated assessment of all ES, for both ES supply and use, in any ecosystem. ES have been valuated through a multitude of individual disciplines and methods (Jacobs *et al.*, 2016), but there is a need for combining relevant value dimensions in integrated assessments of ES (Jacobs *et al.*, 2018), through ecological, economic, and social approaches (Burkhard *et al.*, 2010; Felipe-Lucia *et al.*, 2015; Jacobs *et al.*, 2016). Ecological approaches focus on the ecosystem biophysical properties or the ecological functions (Boeraeve et al., 2015; de Groot et al., 2002); economic approaches give monetary values to ES (Wilson and Carpenter, 1999); and social approaches are based on societal valuation of ES (Martín-López *et al.*, 2012).

[1] See https://www.es-partnership.org/ongoing-discussion-on-the-science-publication-assessing-natures-contributions-to-people-diaz-et-al-2018/

2. Tropical forests: what is at stake?

2.1. Across the tropics

Tropical forests are estimated to host more than two thirds of global terrestrial biodiversity (Gardner *et al.*, 2009). They contribute to major ecological processes, regulate the global climate, and account for one third of the global land-surface metabolic activity (Malhi, 2012). Tropical forests provide numerous ES to hundreds of millions of people (Edwards *et al.*, 2019), and humans have interacted with these ecosystems for tens of thousands of years (Malhi *et al.*, 2014). Moreover, the vast majority of tropical forests are not pristine forests since substantial prehistoric human modifications have been reported worldwide (Willis *et al.*, 2004).

Tropical forest ecosystems are particularly threatened in the Anthropocene, experiencing the combined influence of agricultural conversion, logging, hunting, commercial poaching, and over-harvesting (Gardner *et al.*, 2009; Malhi *et al.*, 2014). These threats result in widespread deforestation (loss of forest cover), forest degradation (loss of ES), and defaunation (loss of wildlife within a standing forest). All tropical regions do not experience the same threats and drivers of tree cover loss (Curtis *et al.* 2018, Song *et al.* 2018). Specifically, among commodity driven deforestation, shifting agriculture, forestry, and wildfire, tree cover loss across tropical Africa is mostly driven by shifting agriculture, while large areas in southern America and in southeastern Asia have been impacted by community driven deforestation (Figure 1.1). Across the tropics, many mammal species are threatened by hunting and are to the brink of extinction (Ripple *et al.*, 2016). Mammal populations are predicted to be partially defaunated in approximately 50% of forests across the tropics (Benítez-López *et al.* 2019). One of the main hotspots of hunting-induced defaunation is located in Cameroon, where more than 50% of all mammal species are estimated to have reductions of populations from 70% to 100% as a consequence of hunting activities (Figure 1.2). Due to global interconnectivity, tropical forests are also profoundly impacted by the introduction of new species and pathogens, and global climate change (Malhi *et al.*, 2014).

The combined impacts of human activities on tropical forests can induce highly variable consequences, depending on many local contextual factors such as the type and intensity of activities, the past and ongoing indirect and feedback effects, and the diversity, structure, and functioning of each specific ecosystem (Malhi *et al.*, 2014). The protection of tropical forests, biodiversity and ES needs a focus on how adequate policy and management strategies can be implemented in order to reach sustainable use and long-term conservation of these ecosystems, at both local and global scales (Edwards *et al.*, 2019).

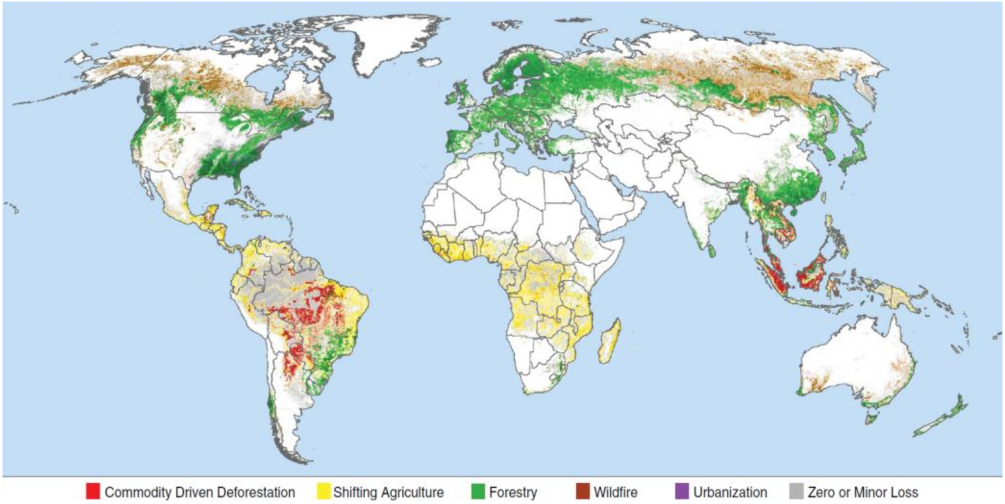


Figure 1.1: Main drivers of forest cover loss from 2001 to 2015 (extracted from Curtis *et al.* 2018).

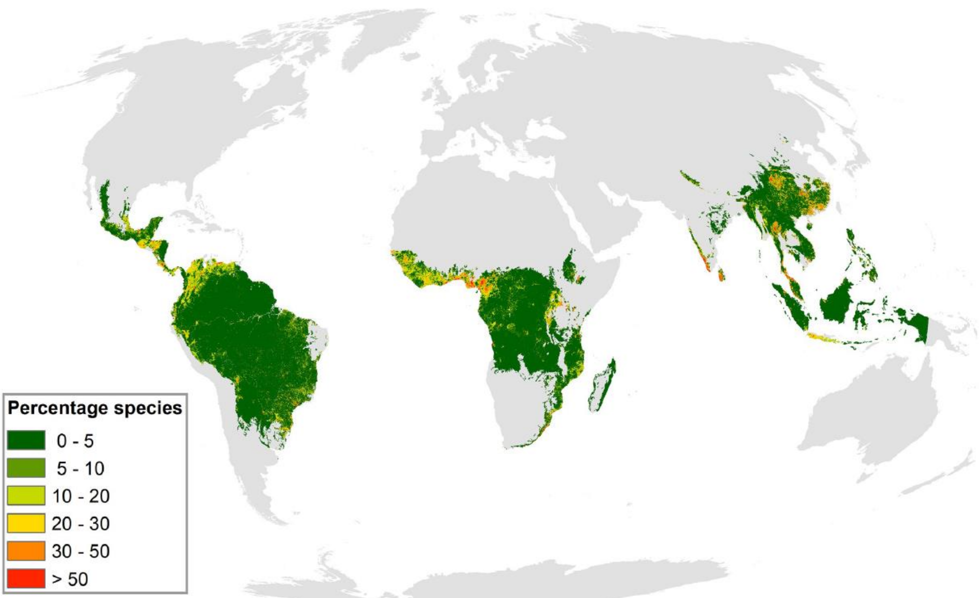


Figure 1.2: Percentage of mammal species (per grid cell) with at least 70% of abundance reductions (extracted from Benítez-López *et al.* 2019).

2.2. In Central Africa

Nearly 113 million people live in Central Africa, among which most rural populations deeply rely on dense forest ecosystems for their livelihoods, characterized by shifting agriculture, hunting and gathering of forest products. Alongside other tropical regions, Central African forests face major environmental threats, namely deforestation, forest degradation, and defaunation (Abernethy *et al.*, 2016).

Compared to other tropical regions, deforestation is relatively low in Central Africa (Achard *et al.*, 2014). Indeed, selective logging has been much promoted rather than large-scale agricultural conversion (Mayaux *et al.*, 2013; Rudel, 2013). Major drivers of deforestation identified in Central Africa are shifting agriculture, firewood production, timber logging, and mining (Abernethy *et al.*, 2016; Gillet *et al.*, 2016b). At continental scale, the impact of shifting agriculture is predominant (Curtis *et al.*, 2018). The dynamics of rural population demography is directly linked to the extent of shifting agriculture, and the needs for forest resources such as wood and wild proteins. An increased accessibility to forest ecosystems also accelerates deforestation and forest degradation (Damania and Wheeler, 2015). The proportion of Central African forest being situated within 10 km of a road has increased from 40% in 1998 (Abernethy *et al.*, 2013) to 53% in 2017 (Koerner *et al.*, 2017). Though selective logging has a moderate impact on deforestation, a side-effect of logging is the opening and fragmentation of continuous forest blocks allowing access to hunters and poachers (Poulsen *et al.*, 2011). In the 2000's, the development of the industrial logging sector in Central Africa lead to a huge expansion of logging roads (Laporte *et al.*, 2007): the total length of the logging road network has doubled from 2003 to 2019 in logging concessions (Kleinschroth *et al.*, 2019). The development of transport infrastructure is projected to become the most important driver of deforestation in the Congo Basin over the next 10 years (Kleinschroth *et al.*, 2019; Megevand, 2013).

Central African forests are particularly defaunated (Benítez-López *et al.*, 2019). Out of 177 vertebrate wildlife species hunted in West and Central Africa (Taylor *et al.*, 2015), 97 are hunted unsustainably (IUCN Red List). The combination of subsistence-based village hunting and commercial poaching constitutes an increasing threat on Central African wildlife (Abernethy *et al.*, 2016). Hunting pressure is related to road density, population density and distance to protected areas (Figure 1.3; Ziegler *et al.* 2016). Overhunting and defaunation profoundly impact the ecological functioning of forest ecosystems (Redford, 1992). In particular, the extirpation of frugivore species has major ecological consequences (Beaune *et al.*, 2013; Omeja *et al.*, 2014) on seed dispersal (Haurez *et al.*, 2015), forest regeneration (Poulsen *et al.*, 2013; Vanthomme *et al.*, 2010), and carbon storage (Brodie, 2016). Current declines in large mammal populations also strongly affect rural food security (Ziegler *et al.*, 2016).

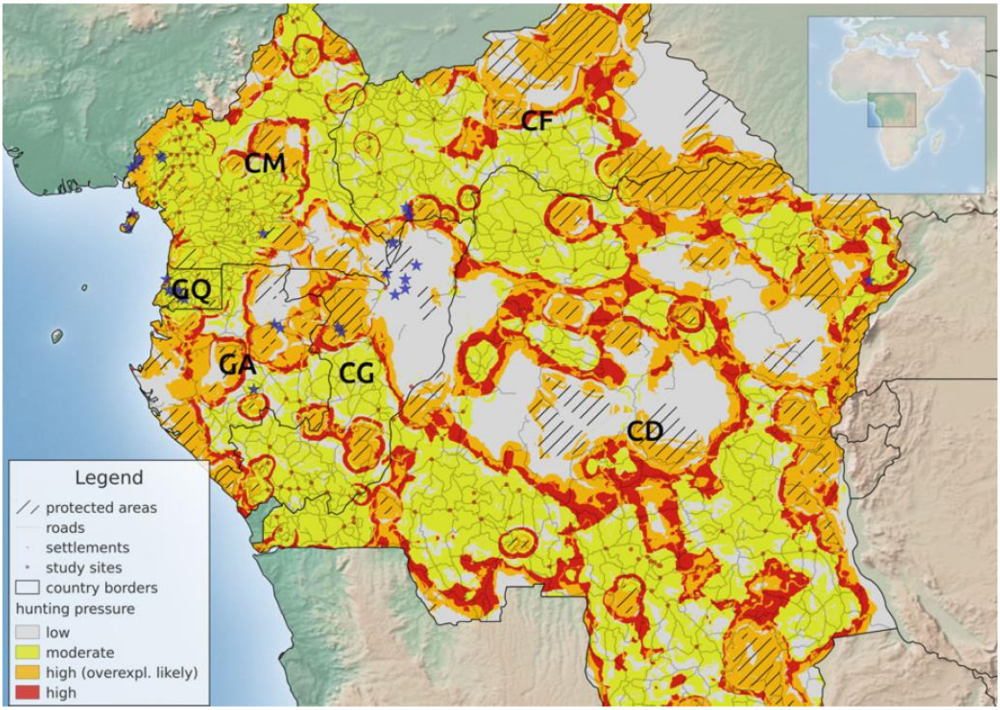


Figure 1.3: Hunting pressure spatially predicted by road density, population density, and distance to protected areas. CM, Cameroon; CF, Central African Republic; CD, Democratic Republic of Congo; GQ, Equatorial Guinea; GA, Gabon; CG, Republic of Congo (extracted from Ziegler *et al.* 2016).

3. Forest land allocations in Central Africa

Tropical forests with high tree cover can seem to be homogeneous when seen from satellite imagery, but they encompass a wide variety of forest management types and allocations that may influence biodiversity and ES. Tropical forests can be perceived differently by different forest stakeholders: conservationists would focus on species-rich and structurally complex ecosystems; logging companies rather value timber stocks; rural populations use the forest as a provider of products and a potential area for shifting agriculture.

In this thesis, the expression ‘forest land allocation’ followed the definition of Oyono *et al.* (2014). ‘Land allocation’ results from a planning and zoning process that identifies explicit geographic areas with allowed practices, including protected areas, logging concessions, or community forests. It differs from ‘land use’ (Oyono *et al.*, 2014) that constitutes the practices concretely implemented by human societies for diverse socio-economic activities (agriculture, selective logging, biodiversity conservation, hunting, etc.).

In Central African countries, namely Cameroon, Central African Republic, Congo, Democratic Republic of Congo, Equatorial Guinea, and Gabon, the land belongs to the States (Karsenty, 2006), which are able to define forest land allocations by delivering specific titles such as protected areas, logging concessions, and community forests. Rural populations generally use forest lands and resources without considering the legal restrictions attributed to forest allocations, and controls from the States are very limited (Nasi *et al.*, 2012). Broadleaf moist forests approximately cover 170 million hectares in Central Africa, among which: 45 million hectares of protected areas (26%; Doumenge *et al.* 2015), 51 million hectares of production forests (30%; FRMi 2018), 2 million hectares of community forests (1%, with the overwhelming majority in Cameroon; Minang *et al.* 2019), and 72 million hectares are not allocated (42%).

In protected areas, the dominant paradigm is biodiversity conservation, recognizing research and tourism as the unique possible activities, while also considering the preservation of regulating services (Nasi *et al.*, 2012). Protection is implemented by governments, with the help of NGOs to enforce protection measures (Abernethy *et al.*, 2016). The ban on agricultural, hunting and gathering activities is a frequent source of conflict with people living in the periphery of protected areas. Central African countries have allocated a higher proportion of their land to conservation than in other tropical regions, with relatively higher conservation success (Laurance *et al.*, 2012). However, commercial poaching is currently raising and dramatically impacts wildlife populations (Bennett, 2011; Nasi *et al.*, 2012; Walsh *et al.*, 2003).

Production forests for timber exploitation, *i.e.*, logging concessions, are attributed by governments to private industrial companies. These concessions can either contribute to responsible forest management through voluntary certification such as Forest Stewardship Council (FSC), or use conventional logging techniques with no consideration of the direct and indirect impacts of logging (Abernethy *et al.*, 2016). FSC-certified logging concessions engage in concrete measures in order to reach economic effectiveness, ecological integrity, and social equity (Forest Stewardship Council, 2012). Production forests under responsible management can play an important role in biodiversity conservation (Clark *et al.*, 2009; Gibson *et al.*, 2011; Nasi *et al.*, 2012; Putz *et al.*, 2012) while also decreasing deforestation (Tritsch *et al.*, 2019). However, FSC certification is scarce in Central Africa and has declined in the recent years (Karsenty, 2019). In Cameroon for instance, FSC-certified forest area decreased from 16% in 2013 to less than 6% in 2019 due to financial difficulties of several European companies. The restricted access and the limited user rights of local populations into logging concessions is often creating negative attitudes towards the logging companies and the state (*e.g.*, Samndong & Vatn 2012).

Community forests in Cameroon are forest areas smaller than 5000 ha, dedicated to the use of local populations (timber, non-timber forest products (NTFP), firewood, hunting, agriculture). However, the forest area really used by forest dwellers is usually much larger than the area of community forests (Lescuyer, 2013; Vermeulen, 2000). Community forests constitute a decentralization of forest management from the state to the local communities (Ezzine de Blas *et al.*, 2011). Most community forests focus on the harvest of timber and NTFP (Ezzine de Blas *et al.*, 2009). The principal objectives of community forests are to improve community engagement in forest management, to enhance forest conservation, and to reduce poverty for forest dwellers (Minang *et al.*, 2019). Implemented after the 1994 Cameroonian Forestry Law, community forestry shows mixed outcome. While it can help communities to generate income and employment, artisanal timber logging does not constitute a reliable economic pathway with the difficult access to the timber market and complicated administrative procedures, and the low contribution to local development and poverty alleviation (Vermeulen, 2014). The effect of community forests in preventing deforestation and forest degradation is also mixed, with highly variable outcome in southeastern Cameroon (Bruggeman *et al.*, 2015).

4. Research strategy

4.1. Research gaps

Central African forests host a substantial biodiversity (Mallon *et al.*, 2015) and supply a multitude of provisioning, regulating, and cultural ES to human populations (de Wasseige *et al.*, 2015). The contributions of these forests to the local livelihoods of more than 60 million people in the context of high-poverty deserve an urgent focus for human well-being and resilience of forest ecosystems. The increasing human pressures on these ecosystems (namely population growth, overexploitation, weak governance, and recent environmental changes, including climate change) will inevitably foster deforestation, forest degradation and defaunation (Abernethy *et al.*, 2016), themselves influencing the biodiversity retained in tropical forests (Gardner *et al.*, 2009) and the ES provided to humans (Igu and Marchant, 2017).

In order to improve the sustainability of forest management in Central Africa, it is first needed to assess biodiversity and ES. Biodiversity and ES are particularly understudied in the tropical forests of Central Africa, compared to other tropical regions (Malhi *et al.*, 2014; Wangai *et al.*, 2016). In particular, no integrated assessment of ES (combining ecological, economic, and social approaches) has been made in this data-deficient region. Most existing studies have focused on individual provisioning ES, whereas cultural services have rarely been addressed (Wangai *et al.*, 2016). Only a few studies conducted integrated ES assessments in tropical Africa, notably in southern African woodlands by identifying human impacts on ES supply (Ryan *et al.*, 2016) and analyzing the interactions between provisioning services and income of rural populations (Pritchard *et al.*, 2019).

Such biodiversity and ES assessments are needed in order to design sustainable forest land planning, management and conservation strategies, in line with the needs and uses of forest stakeholders (Jacobs *et al.*, 2016). Integrated ES assessments are particularly useful to guide concrete strategies towards ecological sustainability, social justice, and economic efficiency (Costanza, 2000; Farley, 2012; Millennium Ecosystem Assessment, 2005). In particular, the integration of all stakeholders in the decision making process allows to legitimize management strategies according to multiple interests (Martín-López *et al.*, 2012; Menzel and Teng, 2009).

Diverse forest allocations may have contrasted potentials for the conservation of biodiversity (Panlasigui *et al.*, 2018; Poulsen *et al.*, 2011) and the supply of ES (Nasi *et al.*, 2011; Plieninger *et al.*, 2015; Wilkie *et al.*, 2019), considering different user rights for rural people’s access to forest resources. Other determinants may also influence biodiversity and ES: proximity to villages (Beirne *et al.*, 2019) and roads (Kleinschroth *et al.*, 2019) could impact biodiversity, whereas land use changes (Quintas-Soriano *et al.*, 2016) and local socio-demography (Carpenter *et al.*, 2006; Zhang *et al.*, 2016) may influence ES. It is essential to decouple and quantify the effects of these potential determinants on biodiversity and ES in order to design adequate management strategies (Poulsen *et al.*, 2011).

4.2. Social-ecological system

This thesis has been conducted in the Dja area, in southeastern Cameroon (East Province, 12°25’ to 14°31’E, 2°49’ to 3°44’N, mean altitude of 743 m), for several reasons. Cameroon is the first country to have implemented a forestry reform in Central Africa (in 1994), including forest management plans and community forests. Three forest allocations of interest (protected area, logging concession, and community forest) are adjacent to each other in the study area (see **Chapter 2**, Figure 2.1), facilitating logistics on the field and more importantly ensuring that potential environmental co-factors are negligible in analyses. Indeed, the three areas belong to the same bioregion (Droissart *et al.*, 2018; Fayolle *et al.*, 2014), and according to available data, the forests show similar tree species composition (Cellule Aménagement Pallisco and Nature+, 2015; Sonké, 1998). Vegetation corresponds to dense forests of the Guineo-Congolian Region (Droissart *et al.*, 2018; White, 1983) and is classified as Moist Central Africa (Fayolle *et al.*, 2014). The mean annual temperature is 23.1°C and the mean annual rainfall is 1640 mm (Hijmans *et al.*, 2005). This allows comparing biodiversity and ES among theoretically similar initial forest ecosystems, with the same climate, but with distinct historical impacts of management. In addition, the main ethnolinguistic group of this area (Makaa-Ndjem group, corresponding to Bantu people) is the most studied in Central Africa, with descriptions of hunting techniques since the colonization period (Koch, 1968) and detailed studies of human pressures on forest ecosystems for hunting, fishing and gathering of NTFP (Delvingt, 2001; Vermeulen, 2000). Such knowledge allows comparing the supply and use of ES with previous studies, notably including historical references.

Three forest allocations dominate the forest area and are together largely represented in Cameroon (88% of the National Forest Estate) and in Central Africa (57% of moist forest areas). This thesis specifically studies (i) a protected area (Dja Biosphere Reserve), (ii) a logging concession (granted to Pallisco company), and (iii) three community forests (Medjoh, Avilso, and Eschiambor). Mean forest cover, deforestation rate and activities allowed to local populations in each forest allocation are given in Appendix 1.

The Dja Biosphere Reserve is a Habitat/Species Management Area (category IV of IUCN protected areas), ‘Man and Biosphere Reserve’ since 1981, and UNESCO World Heritage site since 1987. With a core area of 526 000 hectares, it is the largest protected area of the country, dedicated to the conservation of biodiversity. The Reserve has benefited from the European Union’s support through the ECOFAC programme.

The logging concession has been managed by Pallisco company since 2004, and is FSC-certified since 2008. It is the last FSC-certified logging concession in Cameroon since the abandonment of all other FSC-certified logging companies between 2009 and 2018 due to financial difficulties (Karsenty, 2019). The concession covers 388 949 hectares granted under a management plan of 30 years developed by the company, and approved by the Ministry of Forestry and Wildlife. Timber logging is highly selective with an average of 0.65 stems and 9.6 m^3 harvested/hectare in 2018 in the annual allowable cuts (‘*assiettes annuelles de coupe*’) themselves logged every 30 years. The exploitable timber stocks represent a mean of 3.4 stems and 24.7 m^3/hectare. Management plans project a volume recovery of more than 80% for mainly logged species (Cellule Aménagement Pallisco and Nature+, 2015).

The community forests of Medjoh (4964 ha), Avilso (3433 ha), and Eschiambor (5069 ha) are located between the Dja Biosphere Reserve and the FSC-certified logging concession. They have been launched following the 1994 Forestry Law, based on a simple management plan developed by the community and approved by the Ministry of Forestry and Wildlife. Community forests are dedicated to the use of local populations and aim to improve rural livelihoods.

Of course, all protected areas, all logging concessions and all community forests are not managed in the same manner. All results obtained in this thesis can not be generalized across Cameroon or Central Africa, and they are systematically discussed in the light of evidence reported in other places and contexts, before delineating any broad picture.

The study area is sparsely populated, with a mean of 8 people/km^2 in 2015 (Cellule Aménagement Pallisco & Nature+ 2015; www.citypopulation.de). Local populations are divided into two ethnic groups: Bantu and Baka Pygmy people. In this area, Bantu people are part of the Makaa-Ndjem ethnolinguistic group (zone A80 in the classification of Guthrie, 1948), that comprises Badjoué, Nzimé and Ndjem people. Baka people are indigenous in this area and were present before Bantu people (Winterbottom, 1992). Main activities of local populations comprise shifting agriculture, hunting, fishing, gathering of forest products, and artisanal logging (Vermeulen, 2000).

The local context of the study area constitutes a particular social-ecological system, defined as ‘a particular group of people, a particular set of resources, and a particular set of institutions that operate together’ (Janssen *et al.*, 2007). A social-ecological system results from a co-evolution of ecosystem, economy, culture, technology, and institutional development at different scales (Martens and Rotmans, 2005), allowing the combination of the use of social and environmental sciences in a consistent approach (Ostrom and Cox, 2010). Within a social-ecological system, the resources consumed and their distribution in the population evolve in response to external and internal human influences (Janssen *et al.*, 2007). The differentiated access to ES, the distinctions among categories of ES in their contributions to human well-being, and the internal and external actors are also critical for the understanding of ES use in a specific social-ecological system (Fisher *et al.*, 2014).

Directly linked to the forest allocations previously presented, the social-ecological system studied in this thesis is composed of several groups of stakeholders, who show contrasted interests and needs (Gillet *et al.*, 2016a; Minang *et al.*, 2019):

- Local populations: rural communities who depend on the forests for their livelihoods (Bantu and Baka Pygmy people);
- Logging companies: managers and workers in private companies of timber logging in concessions allocated by the Ministry of Forestry and Wildlife, either certified or not;
- Ministry of Forestry and Wildlife: administration and officials responsible for the implementation of the Forestry Law, the conservation in protected areas, the approval, facilitation and monitoring of forest resources (validation of the management plans of logging concessions and community forests);
- Community forest entities: legal entities managing community forests, mostly composed of local citizens;
- NGOs and associative sector: facilitators for the implementation of community forests, environmental protection, social equity, capacity building, public awareness raising, and communication relays between forest stakeholders;
- Universities and consultants: providers of analytical services to government, local communities, and private sector, providing training, generating and sharing knowledge.

Several conflicts regularly occur among forest stakeholders in southeastern Cameroon, in a context of rampant corruption. In particular, as a consequence of the national forest zoning plan, local populations have lost some traditional customary rights due to frequent overlaps of their zones of forest use with the areas allocated to logging concessions or protected areas (Samndong and Vatn, 2012). The situation is not brighter in community forests, where there are diverse management conflicts with external actors (logging operators, neighboring villages, Forestry administration), or internal conflicts in community forest management entities (Ezzine de Blas *et al.*, 2011). Other major land use conflicts arise from the overlapping of natural resource permits (mining, oil/gas, agro-industrial plantations, and logging) with protected areas, other existing permits, and community forestry, due to different ministries allocating distinct projects to the same zones without appropriate concertation (Schwartz *et al.*, 2012).

While acknowledging the complexity of the studied social-ecological system, only the use of forests by local populations has been considered in this thesis. The following chapters focus on different components of this social-ecological system and provide important insights in the understanding of the local context. In particular, the forest ecosystem is studied in **Chapter 2** and the social context is considered in **Chapters 3** and **4**, through an extensive population census (Appendices 6 and 9) and an analysis of the perceptions and the daily use of ES. The dynamics of land tenure and user rights are beyond the scope of this thesis, but have been addressed by Vermeulen (2000) and Gillet (2016). Allowed and restricted activities in the studied forest allocations are detailed in Appendix 1.

4.3. Conceptual framework and research objectives

The conceptual framework of this thesis (Figure 1.4) is built upon the ES framework (Millennium Ecosystem Assessment, 2005), completed by recent complementary insights, such as the NCP concept (Díaz *et al.*, 2018; Pascual *et al.*, 2017) integrating the importance of culture, indigenous and local knowledge in understanding the links between people and nature. The relevance of ES and NCP typologies is not discussed in this thesis because this debate is out of its scope. The polemics between ES and NCP concepts should not distract researchers from the central challenge of working together to bolster knowledge across disciplines, in order ‘to achieve the fundamental societal and economic changes needed to create a desirable and sustainable future’ (de Groot *et al.*, 2018).

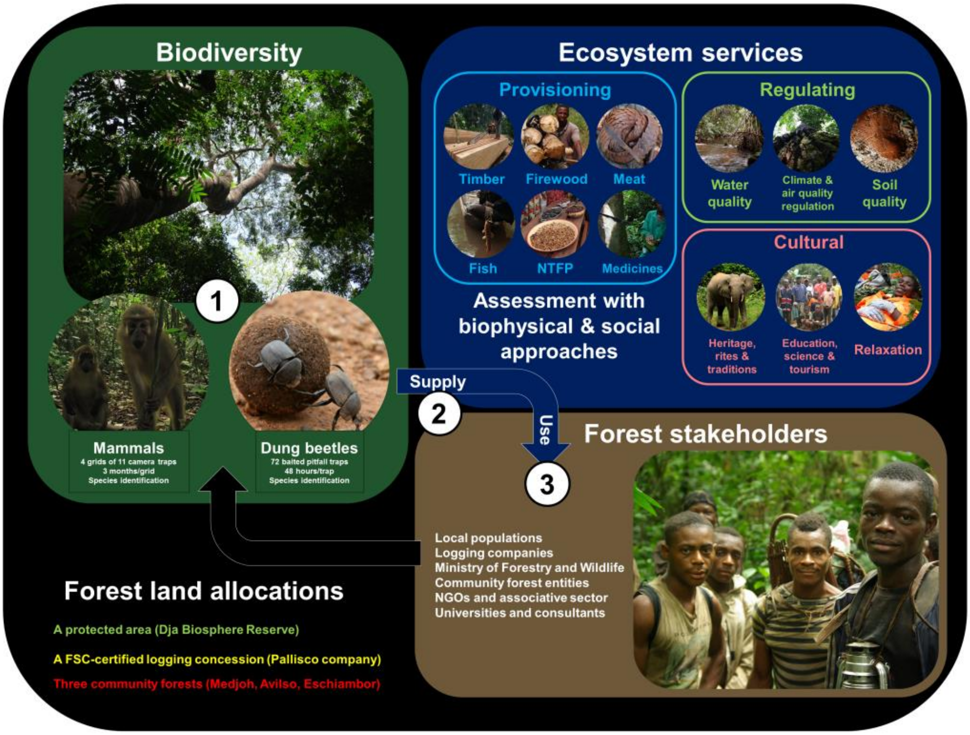


Figure 1.4: Conceptual framework of the thesis, in which the numbers correspond to the specific objectives.

The **general objective** of the thesis is to assess the conservation value of tropical forests in the Dja area, in southeastern Cameroon, as well as the supply of ecosystem services and use by local populations, in three contrasted forest land allocations: a protected area, a FSC-certified logging concession, and three community forests.

The **specific objectives** that are detailed below can be integrated into the conceptual framework (Figure 1.4) relating biodiversity, supply and use of ecosystem services, interactions with forest stakeholders, and the overall influence of forest management through forest land allocations. The first objective is to assess the conservation value of the three forest allocations, and its determinants, through the inventory of two taxonomic groups (mammal and dung beetle species). The second objective is to assess the perceptions of forest stakeholders about the supply of ecosystem services to local populations, and their determinants. The third objective is to assess the use of provisioning and cultural ecosystem services by local populations, as well as its determinants and sustainability.

4.4. Structure of the thesis

In **Chapter 2**, we identified the determinants of the conservation value of tropical forests in southeastern Cameroon, using two taxonomic groups (mammals and dung beetles). Specifically, we disentangled the effects of forest allocation, proximity to human settlements and local habitat on biodiversity. We have inventoried mammals and dung beetles with appropriate sampling methods: 44 camera traps and 72 pitfall traps, respectively. We examined the variation in species richness between and within forest allocations, as well as the uniqueness of species assemblages by partitioning beta diversity into its turnover and nestedness components, and by integrating information on species traits and conservation status in multivariate analyses. Based on our results in the Dja area, we discuss the perspectives for the reconciliation of conservation and forest management in Central Africa. This study has been published in the journal *Biological Conservation*, in an article entitled ‘Conservation value of tropical forests: Distance to human settlements matters more than management in Central Africa’ (Lhoest *et al.*, 2020).

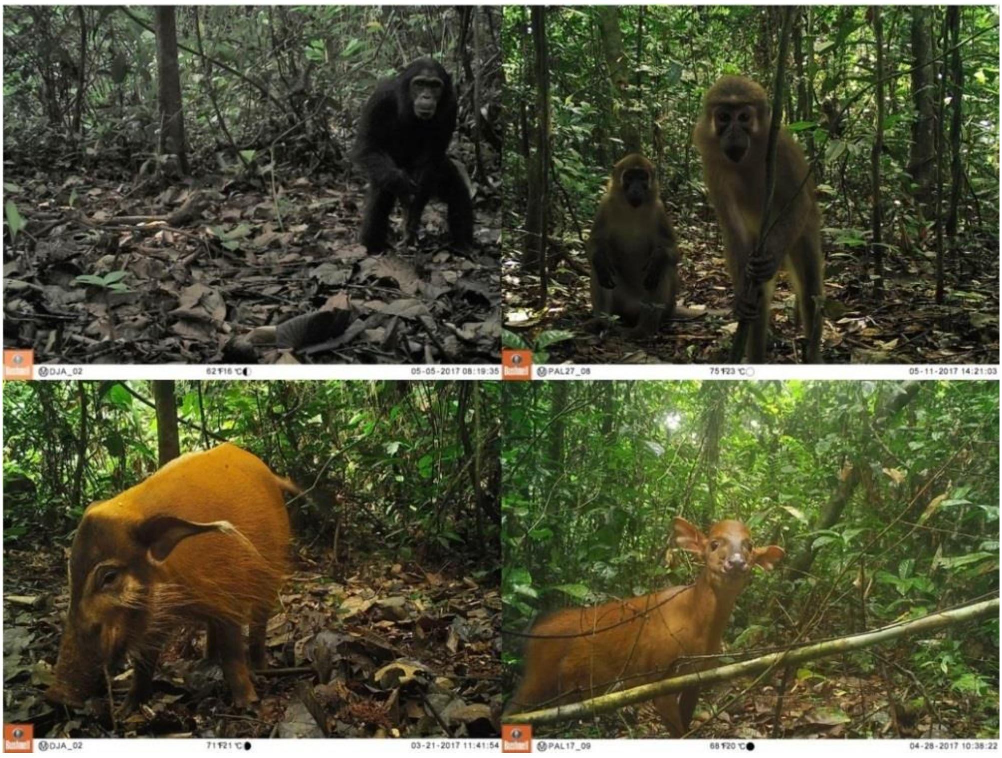
In **Chapter 3**, we give an overview of the ES provided by tropical forests to local populations in southeastern Cameroon, based on the perceptions of various forest stakeholders, acquired through 225 individual interviews. We distinguished the perceptions of ES significance and ES abundance. We also identified the determinants of the perceptions of ES abundance, among forest allocations, past deforestation, and socio-demographic characteristics of respondents. The social approach conducted in this data-deficient region gives insights on the most important and abundant ES for local populations, and helps to set the priorities for integrated ES assessments. This study has been published in the journal *Ecosystem Services*, in an article entitled ‘Perceptions of ecosystem services provided by tropical forests to local populations in Cameroon’ (Lhoest *et al.*, 2019).

In **Chapter 4**, based on the priorities for integrated ES assessments and the most important ES identified in **Chapter 3**, we conducted a detailed monitoring of the use of provisioning and cultural ES by local populations. We have quantified the consumption of bushmeat, firewood and timber (provisioning services) by rural households, and we compare it to sustainability standards. We also mapped the extent of the use of the three provisioning and five cultural services (cultural heritage and identity, inspiration for culture and art, spiritual experience, recreation, and education). We finally identified the influence of potential determinants of ES use (i) at the household scale (socio-demographic characteristics), and (ii) at the village scale (total population size, nearby forest allocations, and deforestation rate). This study has been published in a Special Issue of the journal *Sustainability*, in a manuscript entitled 'Quantifying the use of forest ecosystem services by local populations in southeastern Cameroon'.

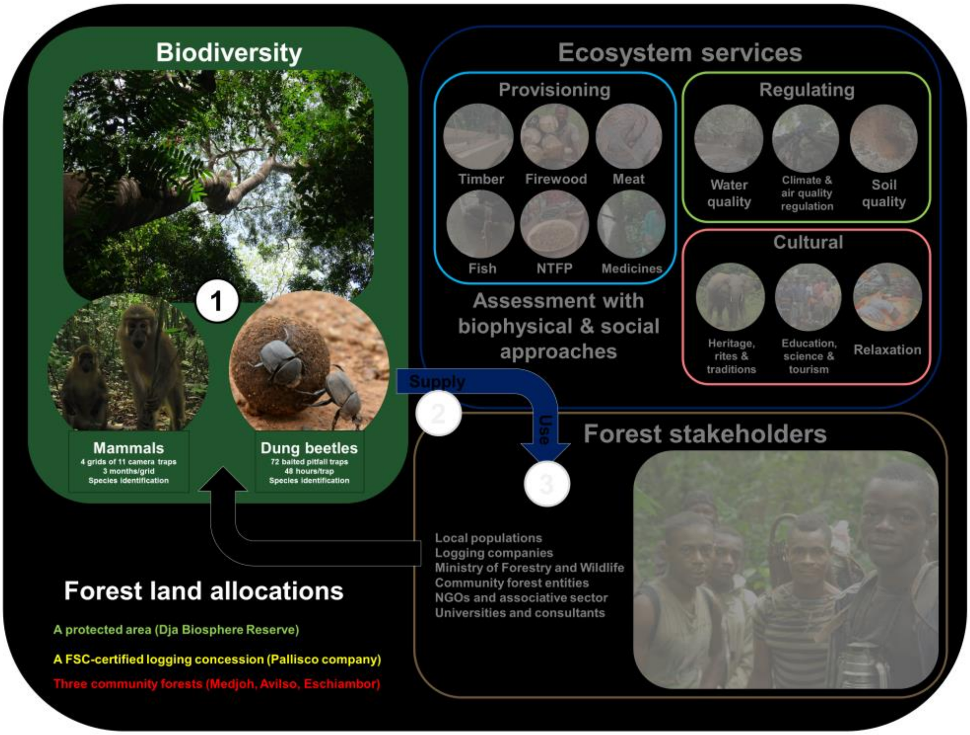
In **Chapter 5**, the main results and achievements of the thesis are summarized. Practical implications for the role of forest allocations are presented. A potential reconciliation between forest conservation and the sustainable use of forest resources is discussed. Methodological feedbacks are given about the use of mammal and dung beetle species as indicators of biodiversity. Research perspectives are developed for studying the interactions between biodiversity and ES. Finally, some insights are given for the concrete integration of the ES concept in tropical forest management.

2

Conservation value of forest allocations



1. Preamble



In this chapter, we aimed to identify the determinants of the conservation value of tropical forests in southeastern Cameroon, by disentangling the effects of forest allocations, proximity to human settlements, and local habitat. We inventoried two taxonomic groups: mammal species with 44 camera traps and dung beetle species with 72 pitfall traps. We used an integrated analytical approach, examining both species richness and composition.

This chapter is adapted from: Lhoest S., Fonteyn D., Daïnou K., Delbeke L., Doucet J.-L., Dufrêne M., Josso J.-F., Ligot G., Oszwald J., Rivault E., Verheggen F., Vermeulen C., Biwolé A. & Fayolle A. (2020). Conservation value of tropical forests: Distance to human settlements matters more than management in Central Africa. *Biological Conservation*, 241, 108351.

2. Introduction

Tropical forests host at least two thirds of the Earth's terrestrial biodiversity (Gardner *et al.*, 2009), while covering only 6 to 7% of the land surface (Dirzo and Raven, 2003). But intensified anthropogenic activities lead to deforestation (loss of forest cover) and forest degradation (loss of ES). These threats induce an irreversible and drastic biodiversity loss across tropical ecosystems (Gardner *et al.*, 2009) with major ecological consequences (Malhi *et al.*, 2014; Poulsen *et al.*, 2013).

In explicit geographical zones, planning and zoning processes define several forest allocations with different allowed practices (Oyono *et al.*, 2014). The area allocated to biodiversity conservation has increased since the middle of the twentieth century (Watson *et al.*, 2014). Despite these efforts, protected areas in the tropics are subjected to an erosion of biodiversity (Laurance *et al.*, 2012; Tranquilli *et al.*, 2014) associated with a rapid human population growth at protected area edges (Wittemyer *et al.*, 2008). Covering a major proportion of tropical areas, production forests may also play a buffering role for biodiversity conservation (Clark *et al.*, 2009; Gibson *et al.*, 2011; Nasi *et al.*, 2012; Putz *et al.*, 2012). Responsibly managed production forests (with a management plan and under reduced-impact selective logging) can harbour a level of biodiversity that is similar to those observed in undisturbed or protected forests in terms of species richness (D. P. Edwards *et al.*, 2014; Gibson *et al.*, 2011; Putz *et al.*, 2012). But all production forests are not managed equally: companies certified by responsible management standards (*e.g.*, Forest Stewardship Council, FSC, or Programme for the Endorsement of Forest Certification, PEFC) are relatively scarce, especially in Central Africa, and many production forests are managed under conventional logging. Engaging local populations in management has also been suggested as an alternative to state-managed conservation in protected areas (Berkes *et al.*, 1994; Duguma *et al.*, 2018; Kellert *et al.*, 2000; Minang *et al.*, 2019). As an alternative to industrial logging in Central Africa, community forests have been shown to contribute to social and economic development with livelihood improvement (Lescuyer *et al.*, 2019). The participation of local communities can improve sustainability if they are aware of the risks of unsustainable management for the long-term provision of goods and services (Blomley, 2013; Maryudi *et al.*, 2012; Ribot, 2003). Different forest allocations pose different threats and opportunities for biodiversity conservation. Thus, the effects of different forest allocations on biodiversity need to be evaluated (Panlasigui *et al.*, 2018), specifically in Central Africa, among protected areas, production forests, and community forests (Poulsen *et al.*, 2011). Besides forest management, the influence of human settlements on biodiversity also needs to be quantified since intensified human activities, such as hunting, agriculture or artisanal logging, are directly associated to proximity to villages (Beirne *et al.*, 2019) and roads (Kleinschroth *et al.*, 2019). These disturbances modify forest ecosystems at the landscape-scale and at the local-scale of species habitat. Decoupling the effects of these different drivers on different groups and at different scales is of high importance for designing adequate conservation strategies (Poulsen *et al.*, 2011).

Quantifying forest conservation value implies considering taxonomic groups sensitive to environmental disturbance and contributing to major ecological processes, such as mammals and insects (Nichols *et al.*, 2009). On the one hand, mammal species are the main target of hunting, leading to a massive defaunation in Central Africa (Abernethy *et al.*, 2016; Ziegler *et al.*, 2016) and many species of iconic megafauna (such as the chimpanzee, *Pan troglodytes*) are classified as endangered on the IUCN Red List (www.iucnredlist.org). The extirpation of hunted species leads to empty forests that still appear structurally intact but where most ecological functions are altered: trophic webs are disrupted, seed dispersal is limited hampering tree recruitment and forest regeneration, and other cascading effects (Abernethy *et al.*, 2013; Poulsen *et al.*, 2018; Redford, 1992; Terborgh *et al.*, 2008). On the other hand, insects are key components of tropical forest ecosystems (Nichols *et al.*, 2008). Specifically, dung beetle species are reported as excellent cost-effective ecological indicators in tropical biodiversity surveys at various scales (Cajaiba *et al.*, 2017; Gardner *et al.*, 2008; Klein, 1989). They are sensitive to even small disturbances such as reduced-impact or selective logging (Bicknell *et al.*, 2014; Nichols *et al.*, 2007; Nummelin and Hanski, 1989). Dung beetles contribute to a variety of important ecological processes including nutrient cycling and fertilization, plant growth, and seed dispersal (Nervo *et al.*, 2017; Nichols *et al.*, 2008).

Our objective was to identify the determinants of the conservation value of tropical forests in southeastern Cameroon. We specifically aimed to disentangle the effects of (i) forest allocation (protected area, FSC-certified logging concession, and community forest), (ii) proximity to human settlements (roads and villages), and (iii) local habitat (forest degradation, canopy openness and distance to the nearest river) on the richness and uniqueness of local biodiversity. We hypothesized that conservation value is mainly driven by human activities rather than by local habitat characteristics, and specifically by forest management and proximity to human settlements. In northern Republic of Congo, Poulsen *et al.* (2011) indeed showed a higher influence of human disturbance (hunting, logging) at landscape-level on animal populations than local-scale effects (forest structure, canopy cover, fruit abundance, topographic and floristic changes). Here, we examine the variation in species richness between and within forest allocations (alpha and gamma diversities) for two taxonomic groups inventoried and sampled using appropriate methods: mammal species with camera traps and dung beetle species with pitfall traps. We also examine the uniqueness of species assemblages by (i) partitioning beta diversity (Baselga, 2010) into its turnover component (spatial replacement of species between sites of completely different compositions) and its nestedness component (loss of species between sites), and by (ii) conducting multivariate analysis (ordination) that integrates information on species traits and conservation status. Based on an integrated and comparative analysis of forest biodiversity in the specific landscape of the Dja area, we discuss the lessons learned for reconciling tropical forest conservation and management at a larger scale, in Central Africa.

3. Material and Methods

3.1. Study area

The study was conducted in southeastern Cameroon (latitude varying from 2°49' to 3°44' N, longitude from 12°25' to 14°31' E, mean altitude of 743 meters). Forests in this area are assigned to Moist Central Africa (Fayolle *et al.*, 2014). The annual rainfall is approximately 1640 mm with two distinct rainy seasons and a mean annual temperature of 23.1°C (Hijmans *et al.*, 2005).

Cameroon was the first country in Central Africa to implement a national zoning plan and to impose management plans for logging concessions and community forests after the 1994 Cameroonian Forestry Law. Three forest allocations (protected area, logging concession, and community forest) are well represented in Cameroon (88% of the National Forest Estate) and in Central Africa (Figure 2.1A and Appendix 1), and are adjacent to each other in the study area (Figure 2.1B). These areas are diversely affected by industrial and artisanal logging, hunting, and shifting agriculture activities (Abernethy *et al.*, 2016; Poulsen *et al.*, 2011).

The Dja Biosphere Reserve is the largest protected area in the country, managed for biodiversity conservation and listed as a Habitat/Species Management Area under IUCN's Protected Area Categories System. It has been listed as a 'Man and Biosphere Reserve' since 1981 and as a UNESCO World Heritage site since 1987. In the core area (526 000 hectares), agriculture, gathering and hunting are prohibited. In the buffer zone (approximately 200 000 hectares but not precisely delimited yet), local populations can engage in non-industrial sustainable activities (Appendix 1).

The logging concession granted to Pallisco company is managed since 2004 under 30-year forest management plans. Timber harvest is highly selective: on average in 2018, only 0.65 stems and 9.6 m^3 were cut per hectare. Out of the 388 949 hectares granted to the company, 341 708 hectares were certified by the Forest Stewardship Council (FSC) in 2008, committing to best practices for: (i) the economic effectiveness and viability of forest management, (ii) the ecological integrity of the forests through reduced-impact logging, protection of wildlife, protection against pollution, and (iii) the social equity for workers and local populations. User rights are given to bordering populations for deadwood and NTFP collection. Hunting activities are highly regulated (see details in Appendix 1).

The community forests (CF) of Medjoh (4964 ha), Avilso (3433 ha) and Eschiambor (5069 ha) are located between the logging concession and the protected area (Figure 2.1B). CFs are small forest areas situated along roads and villages and are dedicated to the exclusive use by local communities for timber harvesting, deadwood collection, NTFP gathering, hunting, and agriculture (Appendix 1). They are managed via a 'Simple Management Plan' written by the communities themselves and under the supervision of the Forest administration.

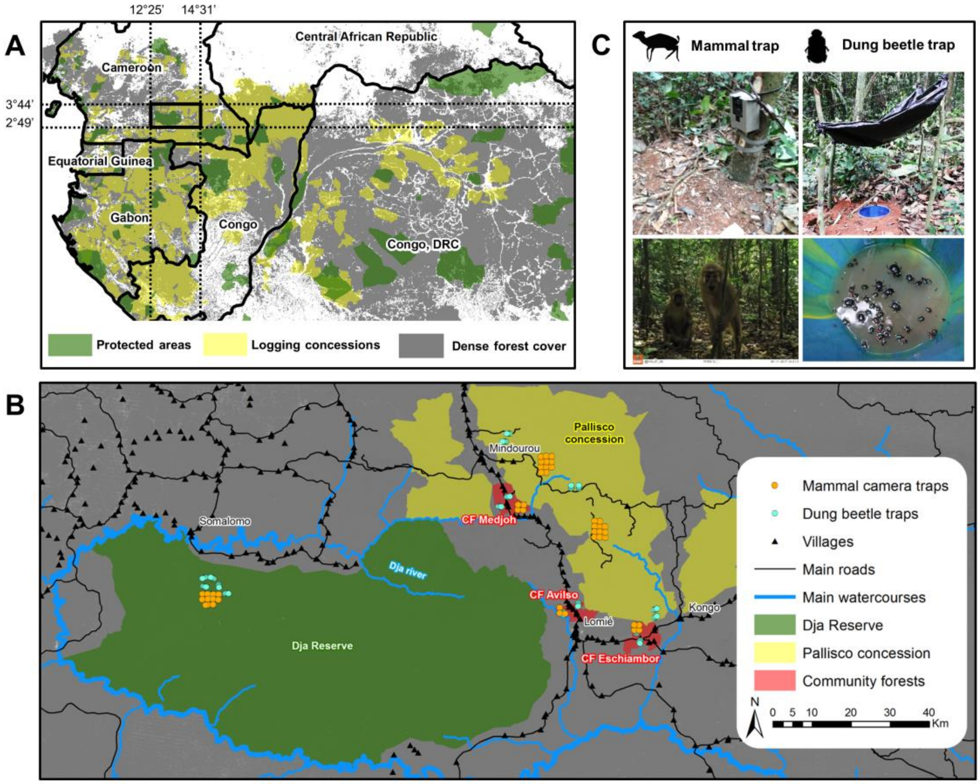


Figure 2.1: (**A**) Location of the study area among logging concessions and protected areas in Central Africa. The grey background corresponds to 'Dense forest cover' and includes lowland, submontane, montane, and swamp forests as defined by Mayaux *et al.* (2004). (**B**) Study area in southeastern Cameroon. Sampling sites of mammals (camera traps) and dung beetles (pitfall traps) in the three forest allocations are shown as orange and cyan points, respectively. (**C**) Illustration of a camera trap (with an example of a picture of Cercocebus agilis) and a pitfall trap (with an example of the individuals collected in a trap after 48 hours of trapping).

3.2. Biodiversity inventory

We inventoried mammals and dung beetles using respectively camera traps (Ahumada *et al.*, 2013) and pitfall traps (Larsen and Forsyth, 2005). Sampling sites were distributed in the three forest allocations, at a distance of at least 500 meters from forest edge. In the logging concession, areas with different logging histories were evenly sampled to consider biodiversity recovery after logging. In the protected area, all sampling sites were located in the northwestern part of the Reserve (Figure 2.1B), where vegetation types are the most similar to the logging concession and community forests (Sonké, 1998).

Mammal species were inventoried using a total of 44 camera traps (model 'Trophy Cam HD Aggressor') set up during the rainy season from February to June 2017 and distributed as follows: one grid of 11 cameras in the protected area, two grids of 11 cameras each in the logging concession (one in a zone logged 23 to 27 years before and the other in a zone logged 17 years before), and one grid of 11 cameras distributed among the three community forests (Figure 2.1B). Distances between two camera grids were between 9.3 and 112.3 km. Cameras were installed at a density of one camera per 2 km² according to the recommendations of the TEAM Network (2011). We placed cameras on trees at 30-50 cm above ground level and oriented in the direction of animal trails with a sufficient field of view to capture full-body images of mammals. The camera-based monitoring lasted 87-99 days and we standardized the data acquired by each camera to the first 87 inventory days. Herbaceous vegetation was systematically cleared in a radius of 4 meters around the camera, insuring comparable detection probability among all cameras. All cameras were set to take three consecutive shots per trigger. After the inventory, we only used the images acquired by 29 cameras (nine in the protected area, five in the zone logged 20-30 years before, nine in the zone logged 10-20 years before, and six in the community forests) because 15 cameras were either stolen/broken or did not operate properly during the entire inventory period. Images obtained from camera traps were analyzed with the Camera Base software linked to Microsoft Access (Tobler, 2015). Detection events separated by at least 10 minutes were considered independent. We identified mammals to species when possible and recorded the number of individuals for each independent detection event. Based on the independent detection events, we produced occurrence and abundance matrices (with species as columns, and either cameras or dates as rows). The mean adult body mass (mean of the body mass given for males and females in Kingdon *et al.,* 2013) and the IUCN status were collated for all inventoried species.

Dung beetles were inventoried using 72 baited pitfall traps from February to April 2016 and distributed along transects of four traps as follows: six transects in the protected area, six transects in the logging concession, and six transects in the community forests (two transects in each community forest). The six transects in the logging concession were distributed as follows: two transects in a zone logged 20 to 26 years before, two transects in a zone logged nine years before, and two transects in a zone logged three years before. To avoid interferences between traps on the same transect, we separated two traps by 250 meters, which is four times the distance recommended by Larsen and Forsyth (2005). Distances between two transects were between 1.4 and 116.9 km. Each pitfall trap consisted of a bucket (280 mm diameter and 270 mm deep) buried flush to the ground, containing one litre of odourless soaped water and baited with 16 grams of human faeces, and protected from rain by a plastic tarp of ~1 m^2. We collected dung beetles after 48 hours and preserved them in 70% ethanol. We identified dung beetles to species when possible and we assigned a unique morphospecies number when identification was uncertain. After having generated a list of all individuals collected, we produced occurrence and abundance matrices (with species as columns and traps as rows). The mean adult body length was computed for all inventoried species and morphospecies.

3.3. Correlates of biodiversity

The values of eight variables were collated for each sampling site, comprising three variables for forest allocations, two variables for proximity to human settlements, and three variables for local habitat. We tested the degree to which these eight variables influenced mammal and dung beetle species richness and composition. For forest allocations, we created three distinct dummy binary variables (i) 'protected area', (ii) 'logging concession', and (iii) 'community forests'. We gave a value of one to the forest allocation to which the sampling site belongs, and null values for the two other forest allocation variables. The proximity to human settlements was computed by: (iv) the distance to the nearest road, and (v) the distance to the nearest village. In terms of habitat variables, we used: (vi) the forest degradation (proportion of pixels classified as degraded forest in the surroundings of each sampling site based on Sentinel-2 satellite imagery and supervised classification; see Appendix 2 for methodological details), (vii) the percentage of canopy openness above dung beetle traps (mean of five values obtained around each trap with hemispherical photographs; see Appendix 2 for methodological details), and (viii) the distance to the nearest river. All distances were computed in meters, with the 'Near' tool in ArcGIS software.

3.4. Biodiversity analyses

All analyses were performed within the R environment (R Core Team, 2018). We used individual-based rarefaction curves (Gotelli and Colwell, 2001) for each sampling site (camera traps for mammals and pitfall traps for dung beetles) to visualize the variation in species richness within and between sampling sites. We also generated sample-based rarefaction curves (Gotelli and Colwell, 2001) to identify any differences in species richness among forest allocations (package 'vegan', Oksanen *et al.*, 2018). We extracted the species richness (alpha diversity) of each sample-based rarefaction curve for a common number of 435 camera-days for mammals and 24 traps for dung beetles for comparison among forest allocations. We also extracted 10 values of species richness for each sampling site from individual-based rarefaction curves, for a number of individuals (or independent detection events for mammals) equal to 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 (for the curves that reached these numbers of individuals). The consideration of ten values of species richness extracted for ten different numbers of individuals allowed to consider the overall shapes of individual-based rarefaction curves rather than only one value of species richness extracted for only one subjective number of individuals. Then, the relationships between the ten values of extracted species richness (response variables) and the eight variables defined above (correlates of biodiversity for mammal and dung beetle sampling sites separately, predictor variables) were analyzed using the sparse Partial Least Squares method (sPLS, using package 'mixOmics', Lê Cao *et al.*, 2009). This method identifies the best predictor variables for species richness of mammals and dung beetles, based on the criterion of the highest Variable Importance in the Projection (VIP). The main advantage of the method consists in the integration and variable selection combined simultaneously in a one-step analysis. In addition, tested variables can be correlated and can contain NA values. Then, Pearson's correlations were computed to further quantify the individual associations between species richness and relevant predictor variables identified by the sPLS.

Based on the occurrence matrix for both mammals and dung beetles, codifying the presence (1) or absence (0) of species (columns) in forest allocations (rows), we partitioned beta diversity into turnover and nestedness components to compare the whole of forest allocations (multiple-site dissimilarities), and pairs of forest allocations (pairwise dissimilarities) using the package 'betapart' (Baselga and Orme, 2012). Whereas the 'turnover' component represent a spatial replacement of species among sites, 'nestedness' and specifically 'nested' sites indicate that some sites constitute a subset of other species assemblages, where some species were lost or are just absent (Baselga, 2010). For mammals, the same number of camera traps were deployed in each forest allocation but ended into slightly unbalanced design because some cameras were stolen or broken in the field. We then developed a bootstrap approach with 1000 iterations to deal with the unbalanced sampling in the camera trap data. For each iteration, we randomly subsampled for each forest allocation five cameras out of the total number of retrieved cameras (up to nine), and we considered the detected species by these five cameras as present in the forest allocation (whatever the number of detections). This allowed generating an occurrence matrix with four lines, corresponding to the forest allocations, and with 26 columns, corresponding to the mammal species. On this occurrence matrix, we computed the multiple-site dissimilarity (among all forest allocations) and the pairwise dissimilarities (among pairs of forest allocations) with their turnover and nestedness components. We finally computed the average for the two beta diversity components (nestedness and turnover) for the two approaches (multiple-site and pairwise) across the 1000 iterations.

In order to visualize the differences in species composition among forest allocations, we performed a Nonmetric Multidimensional Scaling (NMDS), for mammals and dung beetles separately, based on abundance matrices and Bray-Curtis distances (package ‘vegan’, Oksanen *et al.*, 2018). Abundance data were square root transformed and submitted to Wisconsin double standardization, due to large and highly variable abundance values. We plotted sites as triangles (with colors corresponding to forest allocations) and species as points (with size proportional to the mean adult body mass for mammals, and mean adult body length for dung beetles), as well as the IUCN conservation status for mammal species. The eight correlates of biodiversity previously mentioned were also plotted as supplementary variables describing sampling sites.

4. Results

4.1. Species richness

For mammal species, we obtained 3464 independent detection events and identified a total of 26 species (gamma diversity) including iconic species, such as the chimpanzee (*P. troglodytes*) and the giant pangolin (*Manis gigantea*). For dung beetle species, we collected and identified 4475 individuals and identified a total of 71 species (gamma diversity) belonging to 21 genera.

Individual-based and sample-based rarefaction curves for both mammals and dung beetles showed a decrease of species richness from the protected area to the community forests, the logging concession being intermediate between the two (Figure 2.2). Sample-based rarefaction confirmed the slight differences in richness among forest allocations (Figures 2.2B and 2.2D). Individual-based rarefaction curves of the logging concession overlapped with those of the other forest allocations, showing that the logging concession could locally be as rich as the protected area or as depauperate as the community forests. For mammals, the alpha diversity of each forest allocation was 23 species in the protected area, 17 species in the zone logged 20-30 years before, 21 species in the zone logged 10-20 years before, and 18 species in the community forests. For dung beetles, the alpha diversity of each forest allocation was 58 species in the protected area, 49 species in the logging concession, and 41 species in the community forests.

For both mammals and dung beetles, sPLS quantified the relationships between the eight correlates of biodiversity and species richness values derived from individual-based rarefaction curves for 10 to 100 individuals. The most important predictors of species richness were ‘community forests’ (VIP = 1.74, negative correlation) and the distance to the nearest village (VIP = 1.48, positive correlation) for mammal species; the distance to the nearest road (VIP = 1.65, positive correlation) and ‘protected area’ (VIP = 1.58, positive correlation) for dung beetle species (Table 2.1 and Appendix 3).

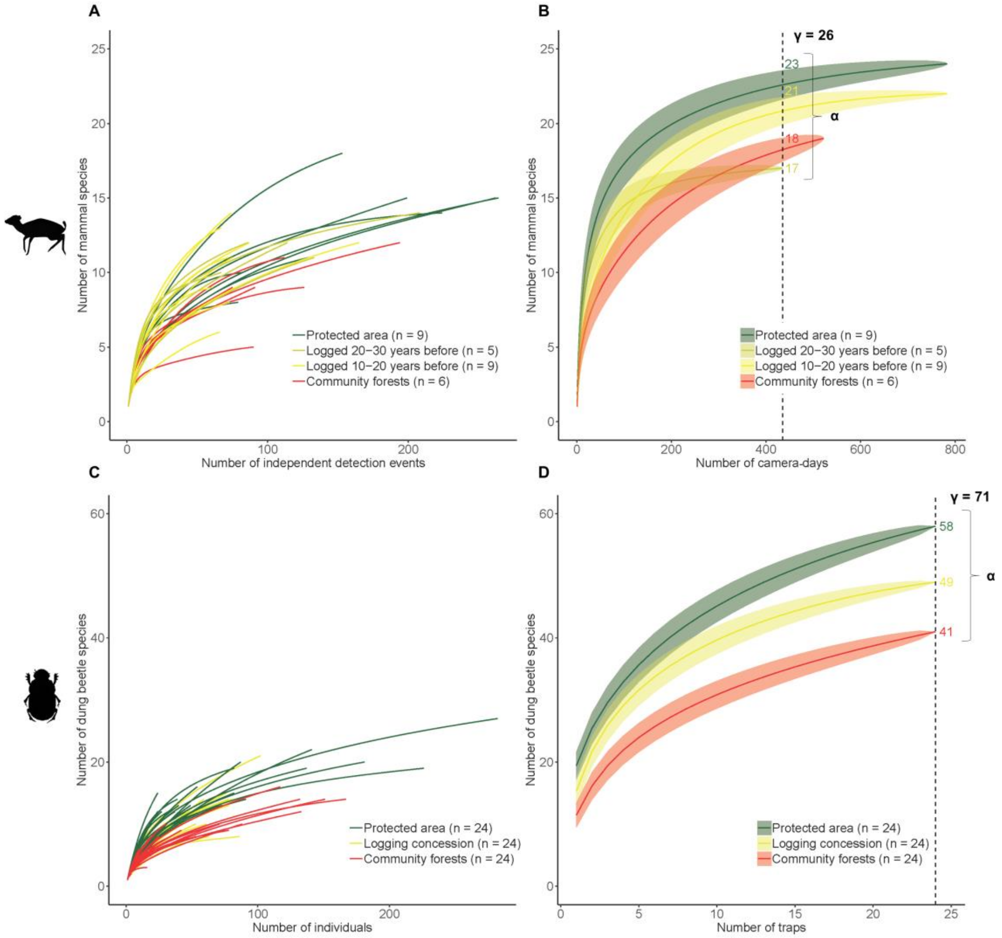


Figure 2.2: Individual-based and sampled-based rarefaction curves for mammals (**A** and **B**) and dung beetles (**C** and **D**). For mammals, the individual-based rarefaction curve considered individuals as the independent detection events (**A**) and the sampled-based rarefaction curve used camera-days on the horizontal axis (**B**). The alpha diversity at the scale of each forest allocation is provided for 435 camera-days (**B**) and for 24 pitfall traps (**D**). The gamma diversity is also provided and comprises the variety of inventoried species for mammals (**B**) and for dung beetles (**D**). The colored shaded areas on sampled-based rarefaction curves (**B** and **D**) correspond to the rarefied species richness ± its standard deviation.

Table 2.1: Values of VIP (Variable Importance in Projection) obtained from the sPLS explaining mammal and dung beetle species richness with correlates of biodiversity. The two highest VIP values are shown in bold for each taxonomic group. The sign in brackets indicate the direction of the effect of each predictor variable on species richness.

	Species richness (Y)	
Correlates of biodiversity (X)	**Mammals**	**Dung beetles**
Distance to the nearest road	0.66 (+)	**1.65 (+)**
Distance to the nearest village	**1.48 (+)**	0.80 (+)
Distance to the nearest river	0.24 (+)	0.44 (-)
Forest degradation	0.24 (-)	0.50 (-)
Canopy openness	/	0.34 (-)
Protected area	0.43 (+)	**1.58 (+)**
Logging concession	1.02 (-)	0.37 (+)
Community forests	**1.74 (-)**	1.21 (-)

4.2. Species composition

Beta diversity was partitioned among forest allocations for both mammal and dung beetle species (Figure 2.3). Among both mammal and dung beetle species, a strong turnover component was revealed, indicating a replacement of species among sites (for mammals, $\beta = 0.25$ with turnover component = 0.15; for dung beetles, $\beta = 0.36$ with turnover component = 0.25). We observed proportionally higher nestedness patterns for mammal species (40% of beta diversity) than for dung beetle species (31% of beta diversity). For mammals, the species composition in the zone logged 20-30 years before the inventory was nested to the species composition in the three other forest allocations, with various levels of turnover. The species composition of the community forests was nested to that of the zone logged 10-20 years before, which was nested to that of the protected area, but showing simultaneously some turnover among forest allocations (list of species in Appendix 4). For dung beetles, the species composition of the community forests was nested to the logging concession, which was nested to the protected area, showing a proportionally higher turnover among forest allocations than mammals (list of species in Appendix 5).

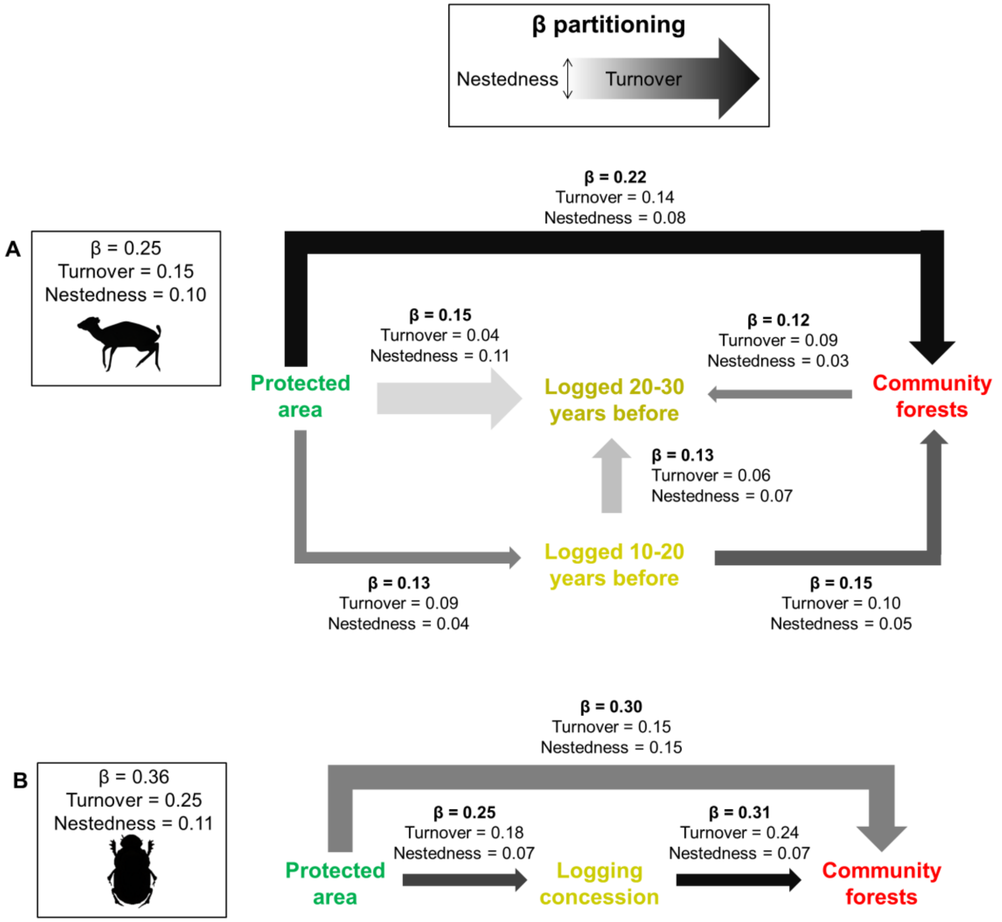


Figure 2.3: Beta diversity partitioning in turnover and nestedness components for mammal species (**A**), and for dung beetle species (**B**). The total beta diversity, turnover, and nestedness values given in the boxes correspond to multiple-site dissimilarities (overall comparisons among forest allocations), whereas other values represent pairwise dissimilarities between two particular forest allocations. The arrows are oriented in the direction of nested sites, with the arrow thickness proportional to the nestedness component, and the arrow darkness proportional to the turnover component.

A clear distinction in species composition between the protected area and the community forests was identified for both mammals and dung beetles, with an intermediate and heterogeneous composition in the logging concession (Figure 2.4). The NMDS for mammal species (Figure 2.4A) showed a clear gradient from degraded community forests associated with mainly rodents and small-bodied species (negative scores on NMDS 1) to richer sites with bigger animals in the protected area and in remote areas from villages (positive scores on NMDS 1). A similar gradient was found for dung beetle species along the first axis (Figure 2.4B), going from degraded forests with high canopy openness (mainly community forests) to remote areas in the logging concession and in the protected area. NMDS stress value was 0.22 for mammals and 0.24 for dung beetles.

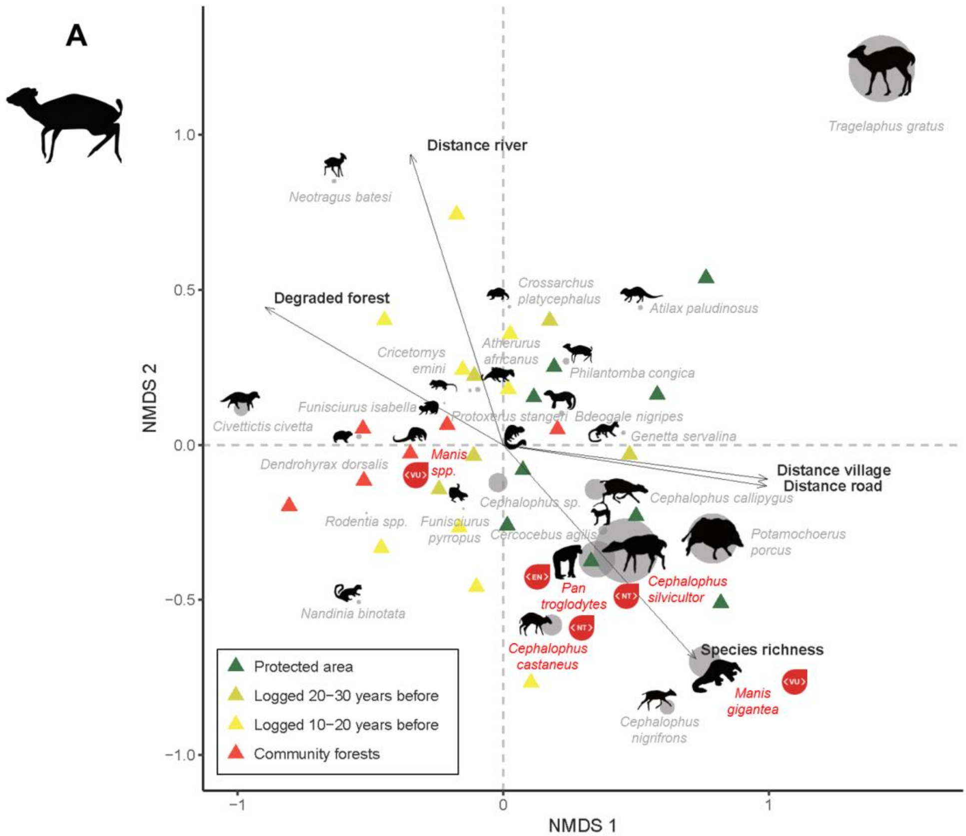


Figure 2.4: Nonmetric Multidimensional Scaling of the abundance matrix for mammal species (**A**) and dung beetle species (**B**) *(see the full legend in page 34).*

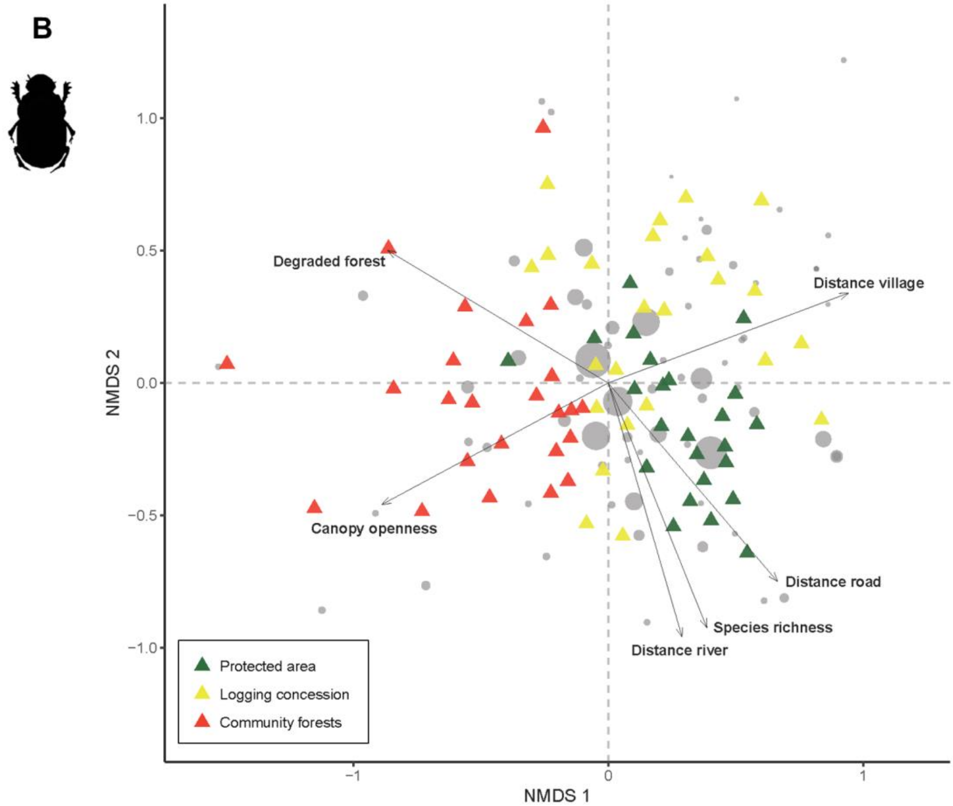


Figure 2.4: Nonmetric Multidimensional Scaling of the abundance matrix for mammal species (**A**) and dung beetle species (**B**). Colored triangles correspond to sampling sites in different forest allocations. Gray points correspond to species, with point size proportional to the mean adult body mass for mammals (**A**) or the mean adult body length for dung beetles (**B**). Arrows show the projection of supplementary variables: distance to the nearest road, distance to the nearest village, distance to the nearest river, forest degradation, canopy openness (only for dung beetles in **B**), and species richness. In **A**, mammal species names written in red are listed in the IUCN Red List of Threatened Species as 'Near Threatened' (NT), 'Vulnerable' (VU), or 'Endangered' (EN), others being assessed as 'Least Concern'. Images of mammal species in **A** are extracted from Kingdon *et al.* (2013).

5. Discussion

Here, we conducted the first cross-taxonomic assessment of the conservation value of diverse forest allocations in Central Africa, using an integrated framework for biodiversity analysis at the landscape scale. We identified an influence of forest allocation on biodiversity patterns. However, proximity to human settlements and disturbance was the main determinant of forest conservation value. We also found differential responses to forest disturbance across mammals and dung beetles.

5.1. Limitations of the study

Due to logistical and financial field constraints, we only sampled a single protected area and a single logging concession and our study design was thus pseudoreplicated (Hurlbert, 1984). Therefore, our results should only be considered and interpreted at the local scale of our study system in its particular social-environmental context in southeastern Cameroon, without any generalization (Cottenie and De Meester, 2003).

The sampling sites were spatially aggregated in grids (camera traps) and transects (pitfall traps) and were not distributed across the entire protected area and logging concession. Then, our sampling sites could not be totally representative of the overall spatial diversity of these two forest allocations. However, it is worth mentioning that we identified a total of 26 mammal species, which is the exact same number of species reported by Bruce *et al.* (2018) in a larger camera trap grid in the Northern Sector of the Dja Reserve. This protected area is reported to host 109 different mammal species of which 35 species are terrestrial and have a body mass higher than 0.5 kg (Kingdon, 2015): we missed some species and some of them are extremely rare and possibly locally extinct.

Our mammal and dung beetle inventory protocols did better detect some species than others, as most inventory techniques do. The ability of camera traps to detect animals is correlated with species body size (Rowcliffe *et al.*, 2011; Tobler *et al.*, 2008). Abundances of small mammal species might have been underestimated, but detection events of mammal species of body mass lower than 1 kg, including mice, rats and squirrels, represented not less than 61% of all detection events. Abundances of semi-arboreal species might also be interpreted with caution, considering that degraded forests may force some species to use the ground more often, such as pangolins (Ingram *et al.*, 2019; Khwaja *et al.*, 2019; Willcox *et al.*, 2019). New methodological perspectives are suggested for considering potential variations in the detectability of some species with camera traps (Fonteyn *et al.*, submitted; Hongo *et al.*, 2020). Concerning pitfall traps, we also used a standardized sampling design which can be used in a wide variety of contexts (Larsen and Forsyth, 2005). All sampling sites were evenly distributed among forest allocations (same sample coverage) with the same sampling protocols and similar conditions. We hypothesized comparable detection probability under closed canopies, though slight differences in forest structure and composition. There is no element in our knowledge that was supposed to modify detection probability among forest allocations and we did everything we could not to influence it. For instance, cameras were oriented toward animal trails, with a clear angle, and with cleared herbaceous vegetation, according to the TEAM Network's recommendations (2011). Thus, we consider that the observed differences among forest allocations revealed true differences in mammal and dung beetle species diversity.

5.2. Differential response of mammals and dung beetles

For mammal species composition, our results showed a loss of species with proximity to human settlements. It was related to a gradient of decreasing body mass and conservation value, with less large and threatened species remaining near villages. As shown by Beirne *et al.* (2019), distance away from villages is directly correlated to hunting pressure. The community forests and the zone logged 20-30 years before were composed of a subset of species present in the more diverse sites and were more strongly impacted by hunting practices because of their proximity to villages. The highly detrimental effect of proximity to hunters' access points (*i.e.*, settlements and roads) has been previously demonstrated up to 40 kilometers inside the forest (Benítez-López *et al.*, 2017), as have the impacts on mammal populations (Benítez-López *et al.*, 2017; Clark *et al.*, 2009; Koerner *et al.*, 2017; Laurance *et al.*, 2006). In the logging concession, the distribution of mammal populations is much more influenced by the development of the logging road network and increased accessibility to hunters and poachers than by the direct effects of logging (Brodie *et al.*, 2015; Robinson *et al.*, 1999; van Vliet and Nasi, 2008). Increasing hunting pressure induces a steady decline in total biomass of all vertebrates, with a particularly rapid decline of large-bodied preferred game species such as primates and ungulates (Koerner *et al.*, 2017; Poulsen *et al.*, 2011), as found here. Only small rodents (Kurten, 2013) and other small generalist species (van Vliet and Nasi, 2008) could be more resilient to hunting pressure (Benítez-López *et al.*, 2017; Koerner *et al.*, 2017; Wright, 2003). Here, and as also observed by Laurance *et al.* (2006) in Gabon, the small mammals (such as rodents) are more abundant in logged forests and forests close to villages than in undisturbed forests. This can be due to the density compensation phenomenon resulting from the extirpation of competitive species (Peres and Dolman, 2000).

Each of the three forest allocations showed distinct dung beetle species composition, indicated by the high turnover component of beta diversity among sampled areas. Large dung beetle species were more abundant in the protected area than in the two other forest allocations. As revealed by our results, several studies also showed that human-driven forest disturbances impact dung beetle species composition, particularly by reducing the abundance of large-sized species (F. A. Edwards *et al.*, 2014; Nichols *et al.*, 2013). Our analyses showed the high local influence of proximity to roads and associated logging, agricultural and habitat disturbances on dung beetle species composition. Dung beetle species have been identified as indicators of closed-canopy forests (Watkins *et al.*, 2017). Impoverished samples of the communities are obtained in any clearings created for road construction, largely degrading dung beetle habitat quality (Hosaka *et al.*, 2014). Dung beetle community composition is also affected by forest fragmentation (Nichols *et al.*, 2007), as seen here in degraded community forests impacted by agriculture and with relatively higher canopy openess. In contrast to mammals, dung beetles are known to be particularly sensitive to the environmental effects of selective logging (Bicknell *et al.*, 2014). As shown here, a negative influence of roads on dung beetle populations has already been demonstrated up to 170 meters into the forest interior due to micro-habitat variation, with associated declines of ecological functions (Edwards *et al.*, 2017; Hosaka *et al.*, 2014) such as dung and seed removal (Andresen, 2003; Slade *et al.*, 2011).

5.3. Conservation value of forest allocations

In the face of major environmental issues in Central Africa (Abernethy *et al.*, 2016), our results confirmed the importance of protected areas in the conservation of large-bodied and threatened mammal species, as well as most forest dung beetle species (as also shown by Davis and Philips, 2005). Even if many protected tropical forests experience alarming biodiversity losses (Laurance *et al.*, 2012), the long-term presence of conservation activities can reduce threats (Tranquilli *et al.*, 2014). In the Dja Biosphere Reserve, conservation activities include law enforcement through anti-poaching patrols and awareness campaigns, scientific research, and tourism, which together can lower threats in African protected areas (Tranquilli *et al.*, 2014). Additionally, in the northern sector of the Reserve motor vehicles cannot easily cross the Dja River reducing accessibility for commercial poachers.

We found that production forests can harbour similar species richness and composition to that of protected areas. Vulnerable pangolin species (*Manis* spp.) were even found more frequently in the logging concession than in the two other forest allocations (Appendix 4). It has already been demonstrated that selective logging has modest impacts on most taxonomic groups (*e.g.*, species richness of birds, mammals, invertebrates, and plants according to Putz *et al.*, 2012) and only slightly reduces biodiversity levels (Clark *et al.*, 2009; Gibson *et al.*, 2011). In particular, Burivalova *et al.* (2014) suggested that most taxonomic groups would be resilient to selective logging at intensities lower than 10 m^3 ha^{-1}, as applied in the FSC-certified concession studied here. However, here we reported high spatial heterogeneity of biodiversity in the logging concession that we related to local disturbances induced by roads. Indeed, as a side effect of logging, the road network can make some areas highly accessible and deeply impacted by human activities (logging, hunting and poaching), whereas remote areas remain nearly intact (Poulsen *et al.*, 2009).

Community forests were found to be particularly depauperate, with a dominance of small-sized mammal species and poor dung beetle communities. The low conservation value of these forests is due to the high proximity to villages and roads (Beirne *et al.*, 2019). Human presence is associated with hunting pressure, fire, and forest fragmentation induced by shifting agriculture. Yet some mammal species were found to be more abundant in these young secondary forests, such as the African palm civet (*Nandinia binotata*) that lives in umbrella trees (*Musanga cecropioides*). Community forests cannot yet be considered as totally defaunated, even though human populations intensively use them for a multitude of ES, including bushmeat provision (Lhoest *et al.*, 2019).

5.4. Conservation implications

Our results confirm that the road network and associated forest accessibility have major detrimental effects on biodiversity. The area damaged by logging roads typically reaches 0.6 to 8.0% of forest area in tropical countries (Kleinschroth and Healey, 2017) and 1.26% in the studied logging concession in 2018. Roads are a financially costly element of logging activities, and both concession holders and biodiversity conservation would benefit to improve the design and planning of logging roads (Edwards *et al.*, 2017). It has been previously suggested to: (i) implement strategic planning and long-term spatial prioritization (Kleinschroth *et al.*, 2019) in order to limit the size and expansion of logging road networks (Laurance *et al.*, 2009; Putz *et al.*, 2008); (ii) define a minimum volume of timber extracted per unit length of logging road to justify road construction (Edwards *et al.*, 2017); (iii) close logging roads after timber extraction to facilitate forest recovery and discourage hunters from penetrating the forest (Bicknell et al., 2015; Clark et al., 2009; Kleinschroth et al., 2016); and (iv) avoid building any roads suitable for motor vehicles inside protected areas (such as in the Dja Biosphere Reserve) and only planning appropriate pedestrian access where needed.

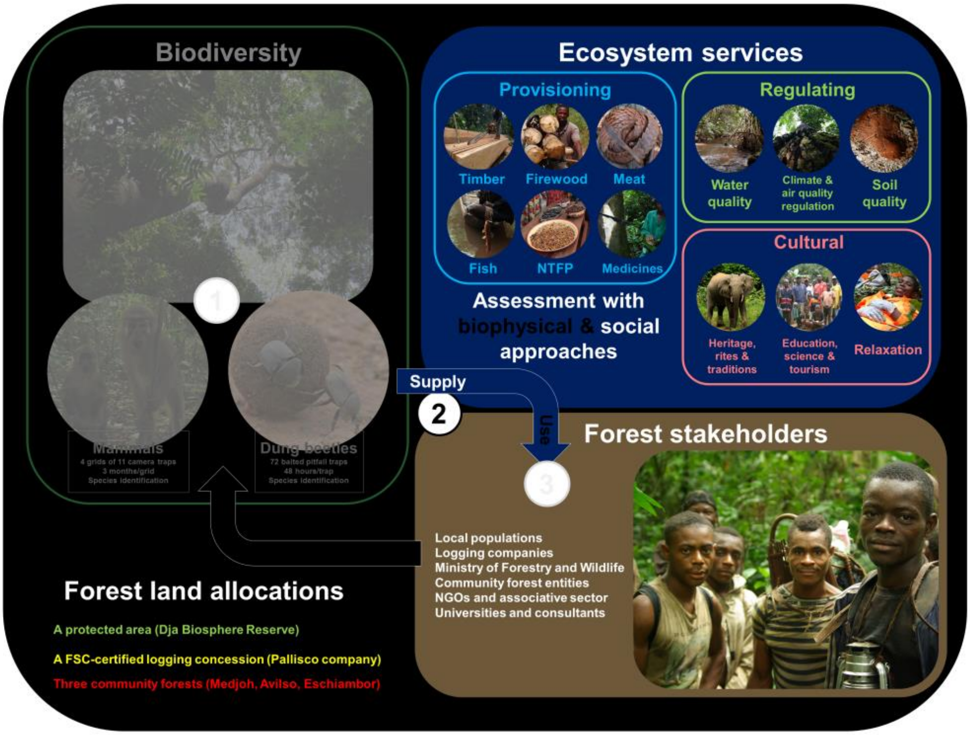
Our study identified a strong decline of mammal species richness in proximity to villages in southeastern Cameroon. The hunting pressure surrounding rural communities is known to be extremely high in Cameroon. Several effective solutions must be implemented to halt the defaunation crisis in Central Africa, including: (i) law enforcement (Critchlow *et al.*, 2017) comprising anti-poaching operations (Benítez-López *et al.*, 2017) and a better control of access in logging concessions and protected areas (van Vliet and Nasi, 2008); (ii) participatory repressive enforcement program (Beirne *et al.*, 2019; Clark *et al.*, 2009; Vermeulen *et al.*, 2009); (iii) ban of hunting of sensitive species (according to the IUCN status) and regulation of hunting of the most resilient and locally abundant species such as the blue duiker (*Philantomba monticola*) or the African brush-tailed porcupine (*Atherurus africanus*) (Nasi *et al.*, 2011; van Vliet and Nasi, 2008); (iv) provision of alternative sources of proteins (local fish farming, aviculture, supply of butcher's meat, vegetal proteins, edible insects) at affordable prices, with a minimization of their negative environmental impacts (Rentsch and Damon, 2013; Wilkie *et al.*, 2005).

Conservation strategies have to be designed and coordinated at a large scale (landscape, national or continental scale) in balance with the need for economic development and bushmeat provision (Poulsen *et al.*, 2011). High values of turnover among forest allocations for both mammal and dung beetle species in our results support a devotion of conservation initiatives to a large number of different sites, with a priority on protected and remote areas of high biodiversity. Production forests in the surroundings of protected areas have a crucial buffer role to play. In particular, adapted management aimed at minimizing the degradation of high conservation value forests is an important requirement of FSC certification. If strictly protected forest patches are not connected with production forests in a larger forest matrix, no conservation intervention is likely to be sufficient (D. P. Edwards *et al.*, 2014). Connected to protected areas, production forests offer the chance to conserve many ES, functions, and species (Clark *et al.*, 2009). They cover a high proportion of forest lands and show lower opportunity costs than protected areas. It is vital for biodiversity that protected and production forests be maintained as forest lands rather than being converted to agriculture or plantations characterized by much lower conservation values (Chazdon *et al.*, 2009).

3

Perceptions of ecosystem services supplied by tropical forests to local populations

1. Preamble



In this chapter, we assessed the perceptions of the supply of ES by tropical forests to local populations in the three studied forest allocations. We conducted a questionnaire survey with 225 forest stakeholders (social approach), combining an open-ended question and 16 directed questions to evaluate the perceptions of ES significance and abundance, respectively.

This chapter is adapted from: Lhoest S., Dufrêne M., Vermeulen C., Oszwald J., Doucet J.-L. & Fayolle A. (2019). Perceptions of ecosystem services provided by tropical forests to local populations in Cameroon. *Ecosystem Services*, 38, 100956.

2. Introduction

Ecosystem services (ES) are the contributions of ecosystems to human well-being (Burkhard *et al.*, 2012). They classically include provisioning, regulating, and cultural services (de Groot *et al.*, 2010). ES constitute a conceptual tool that integrates human-nature relationships (Turner and Daily, 2008) and contributes to the implementation of concrete policies and practices for the sustainable use of all ecosystems.

In order to guide decision makers towards ecological sustainability, economic efficiency, and social justice, any complete ES assessment should use an integrated approach that combines relevant methods (Costanza, 2000; Farley, 2012; Millennium Ecosystem Assessment, 2005). Integrated valuations combine ecological, economic, and social approaches (Burkhard *et al.*, 2010; Felipe-Lucia *et al.*, 2015; Jacobs *et al.*, 2016). Ecological approaches measure the ecological functions or ecosystem biophysical properties (Boeraeve et al., 2015; de Groot et al., 2002); economic approaches give values to ES in monetary terms (Wilson and Carpenter, 1999); and social approaches focus on the values that society attributes to each ES (Martín-López *et al.*, 2012). Current ES assessments mainly focus on the ecological and/or economic approaches (Satz *et al.*, 2013), whereas social approaches are rarely implemented (Boeraeve et al., 2015; Kremen and Ostfeld, 2005). However, social approaches are fundamental to better understand complex social-ecological systems (Orenstein and Groner, 2014). To ensure optimal provision of ES on which humans rely (Rosenberg and McLeod, 2005), it is essential to integrate all stakeholders' perceptions in sustainable management strategies and decisions (Braat and de Groot, 2012; Castro *et al.*, 2011; Collins *et al.*, 2010). The decision making process should incorporate the societies' perceptions in order to: (i) legitimize strategies and decisions, meeting multiple stakeholders' interests (Martín-López *et al.*, 2012; Menzel and Teng, 2009); (ii) anticipate likely reactions, behavior, and compliance of key stakeholders to new regulations and measures (Gelcich *et al.*, 2009; Gelcich and O'Keeffe, 2016; Hicks and Cinner, 2014); and (iii) identify agreement areas (Hicks *et al.*, 2013).

Each ES assessment should be initiated with a social approach to consider the perceptions of local stakeholders (Cuni-Sanchez *et al.*, 2016); furthermore, social methodologies to assess ES are currently disparate (Felipe-Lucia *et al.*, 2015; Menzel and Teng, 2009) and standard approaches need to be developed. Santos-Martín *et al.* (2017) reviewed seven methods that are frequently used in ES literature, dealing with different data types adapted to several valuation purposes: preference assessment (*e.g.*, Martín-López *et al.*, 2012), time use method (*e.g.*, García-Llorente *et al.*, 2016), photo-elicitation surveys (*e.g.*, García-Llorente *et al.*, 2012), narrative methods (*e.g.*, Kovács *et al.*, 2015), participatory mapping (*e.g.*, Plieninger *et al.*, 2013), scenario planning (*e.g.*, Bohensky *et al.*, 2006), and deliberative methods (*e.g.*, Karjalainen *et al.*, 2013). Despite an ongoing debate on ES and nature's contributions to people (NCP) concepts, raised by Díaz *et al.*

(2018), we adopted the ES framework while integrating social approaches in assessments, and emphasize the importance of doing so.

Central Africa is home to approximately 113 million people, with more than 23 million living in Cameroon (Abernethy *et al.*, 2016). Central African forests provide a diversity of provisioning, regulating, and cultural ES, offering wood and means of subsistence to 60 million people living either inside or in the vicinity of forests (de Wasseige *et al.*, 2015), particularly through hunting and gathering non-timber forest products (NTFP). These forests also constitute large carbon stocks that influence global climate (Pan *et al.*, 2011), and host an important part of the world's terrestrial biodiversity (Mallon *et al.*, 2015). Human populations also attribute a variety of socio-cultural values to Central African forests (Vermeulen, 2000). Although deforestation rates are still relatively low in Central Africa in comparison to other tropical regions (Achard *et al.*, 2014), these forests will face multiple human pressures in the near future (Malhi *et al.*, 2014). Environmental changes could soon be observed due to increasing human populations, demand for economic growth, global climate change, overexploitation, and weak governance (Abernethy *et al.*, 2016).

Local-scale assessments of multiple ES provided by Central African tropical forests are urgent and crucial, but none have been made yet (Wangai *et al.*, 2016). These complex social-ecological systems are influenced by several groups of stakeholders with contrasting interests and uses of resources (Gillet *et al.*, 2016a; Janssen *et al.*, 2007), and constitute a high-priority stake considering their contribution to human life quality in a high-poverty context. For the maintenance of future ES flows and sustainability objectives for forest land management, assessment of both ES significance and abundance is required. It is also essential to comprehend how the stakeholders' perceptions of ES are shaped by their surrounding environment (Hartter *et al.*, 2014; Quintas-Soriano *et al.*, 2016) such as forest land allocation and deforestation, and by socio-demographic characteristics (Carpenter *et al.*, 2006; Zhang *et al.*, 2016) to properly align forest land planning strategies (protection, production, or community management) with stakeholders' needs and uses in a sustainable manner.

The main objective of this study was to assess the perceptions of ES provided by tropical forests to local populations in southeastern Cameroon. We specifically aimed to: (i) assess the significance and abundance of ES; and (ii) identify any differences in the perceptions of ES abundance among three forest land allocations (a protected area, a logging concession, and community forests), among areas with different deforestation rates in previous years, and among respondents with distinct socio-demographic characteristics (gender, age, ethnicity, and main occupation). Hereafter, we define the 'perceptions' of ES as the cognition of usefulness and interests of the forest for its contributions to the well-being of local human populations (Attneave, 1962). We consider 'land allocations' as resulting from a planning and zoning process identifying explicit geographical areas with allowed practices (Oyono *et al.*, 2014).

We hypothesize that ES abundance varies among contrasting forest land allocations, considering the differences in access to forest resources and user rights for local populations. Using a social approach with novel data in a data-deficient region, our study provides insights on the importance and perceived supply of ES, and the ability of contrasting forest land allocations to provide abundant ES to local populations. It also contributes significantly in the understanding of the socio-demographic characteristics shaping the ES perceptions of forest stakeholders in rural areas of a developing country in Central Africa.

3. Material and methods

3.1. Study area

The study area was located in southeastern Cameroon, between latitude 2°49'N to 3°44'N and longitude 12°25'E to 14°31'E (Figure 3.1). The annual rainfall is around 1,640 mm with two distinct rainy seasons (August to November, and March to June), the mean annual temperature is 23.1°C (Hijmans *et al.*, 2005). Forests are assigned to Moist Central Africa (Fayolle *et al.*, 2014) and were originally described as a transition type between lowland evergreen and semi-evergreen forests (Letouzey, 1985). In this area, local populations mainly comprise Bantu people, whereas the Baka Pygmy people constitute another smaller ethnolinguistic group. The Baka are considered as the Indigenous population, who were present in the forest even before the arrival of Bantu people (Winterbottom, 1992). Among the Bantu, three ethnolinguistic groups are considered native to the study area: Badjoué, Nzimé, and Ndjem. These are all part of the Makaa-Ndjem ethnolinguistic group, corresponding to the coded Zone A80 in the Guthrie classification of languages (Guthrie, 1948). They pursue similar production systems: shifting cultivation, hunting, fishing, and gathering of forest products (Vermeulen, 2000). We define 'local populations' as rural communities depending on the forests for their daily activities (Bantu and Baka Pygmy populations), and 'forest stakeholders' as all members of the forestry sector (comprising local populations as well as managers, workers, or officials).

According to the World Resources Institute (2012), the classified area of the National Forest Estate (NFE) represented 37% (17.5 million hectares) of Cameroon in 2011. We worked in specific locations (Figure 3.1) associated with the three major land allocations of Cameroonian tropical forests: (i) protected areas (42% of the NFE); (ii) logging concessions divided in forest management units (FMUs, 40% of the NFE); and (iii) community forests (6% of the NFE), representing in total 88% of the NFE. These forest land allocations are also largely represented in Central Africa, at the regional scale. Estimated area, mean forest cover, deforestation rate, and the legal and illegal activities in each forest allocation are mentioned in Appendix 1.

(i) The protected area studied was the Dja Biosphere Reserve, which is the largest protected area in the country and aims to conserve biodiversity according to a management plan approved by the Forestry Administration. It is a ‘Man and Biosphere Reserve’ since 1981, listed as a UNESCO World Heritage site since 1987, and is defined as the IV-category of IUCN protected areas. The Reserve comprises a core area of nearly 526,000 hectares in which agricultural, gathering and hunting activities are prohibited. In the buffer zone (not yet precisely delimited), local populations can pursue non-industrial sustainable activities such as wood collection, NTFP gathering, and shifting agriculture (Appendix 1). According to the Conservation Service and local guides, between 15 and 100 tourists annually visit the northern part of the Reserve where this research was conducted. Tourists are interested in discovering local Baka traditions and major wildlife species such as forest buffalo (*Syncerus caffer nanus*), chimpanzee (*Pan troglodytes*), giant pangolin (*Manis gigantea*), elephant (*Loxodonta cyclotis*), mantled guereza (*Colobus guereza*), leopard (*Panthera pardus*), or western lowland gorilla (*Gorilla gorilla gorilla*). This area is also included in the Dja Biosphere Regional REDD+ Project, which aims to reduce deforestation and forest degradation on 1.2 million hectares of forests in and around the protected area. Previous awareness campaigns for wildlife conservation were conducted under the European ‘ECOFAC’ program.

(ii) The logging concession studied was certified by the Forest Stewardship Council (FSC) in 2008, and has been managed by Pallisco company (http://www.pallisco-cifm.com) since 2004. The company develops forest management plans for their concession areas with a 30-year planning approved by the Forestry Administration (Cellule Aménagement Pallisco and Nature+, 2015). The main timber species selectively logged are sapelli (*Entandrophragma cylindricum*), tali (*Erythrophleum suaveolens*), okan (*Cylicodiscus gabunensis*), and ayous (*Triplochiton scleroxylon*). Nearly 341,000 hectares of the Pallisco logging concession are FSC-certified, with FSC standards applied to ensure economic effectiveness and viability of forest management; ecological integrity of the forests (*i.e.*, reduced-impact logging, protection against pollution, protection of wildlife); and social equity. The social program includes a supply of complete security equipment, health care, accommodation, social security cover, and training for workers. The bordering rural populations are also supported through the Area Fee distributed to local councils, communication and education, creation of a consultation framework, and social realizations such as housing improvement, construction of water wells, boreholes, and classrooms or donation of school supplies. There is no tourist activity in the logging concession. Local populations benefit from user rights for NTFP and deadwood collection in 98% of the concession area, and hunting activities are authorized for self-consumption, with traditional selective techniques, and only for non-protected species (see details in Appendix 1).

(iii) The three community forests (CF) that we studied – Medjoh (4,964 ha), Avilso (3,433 ha), and Eschiambor (5,069 ha) – are located between the protected area and the logging concession. The CF were created in the country after the 1994 Cameroonian Forestry Law with the objective of improving rural livelihoods by increasing monetary revenues, village infrastructures, forest self-management empowerment, and rural employment (Ezzine de Blas *et al.*, 2011). CF are dedicated to exclusive use by village communities (*i.e.*, for timber harvesting, hunting, NTFP gathering, deadwood collection, or agriculture). They are managed with a simple management plan written and implemented by the community itself, after the approval and under the control of the Forestry Administration.

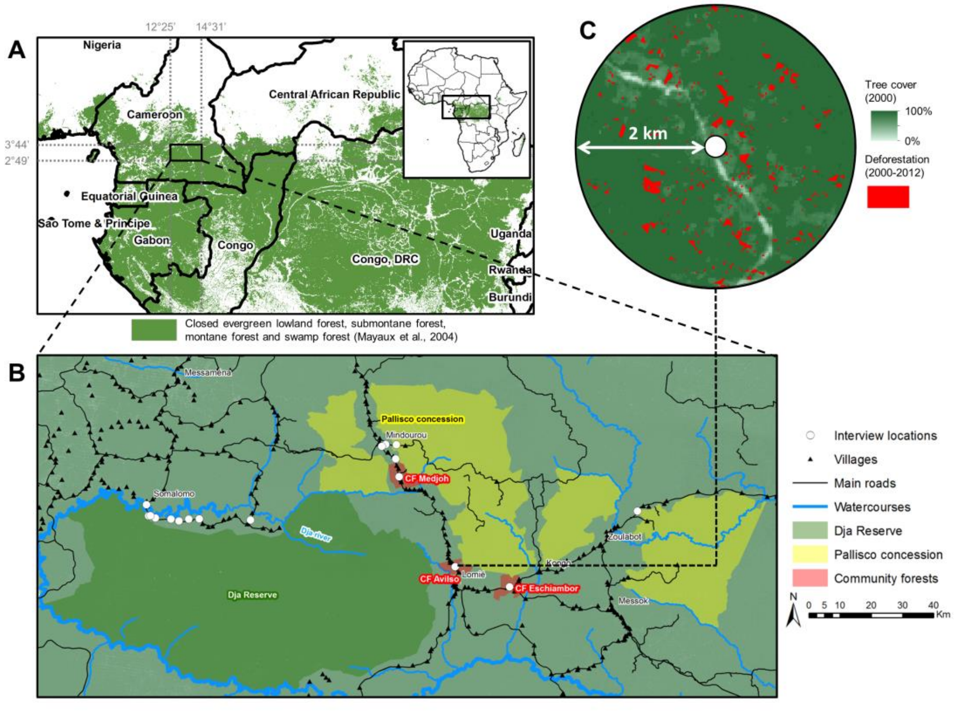


Figure 3.1: Location of the study area in Central Africa (**A**). Sampling locations of interviews in the study area (white dots), associated with the three forest allocations (a protected area, a FSC-certified logging concession, and three community forests) (**B**). Example of a sampling location in a community forest, with 4% of deforested areas between 2000 and 2012 (red polygons; Hansen *et al.*, 2013) in a radius of 2 kilometers (**C**).

3.2. Sampling strategy

We interviewed a total of 225 respondents, distributed into three groups of 75 forest stakeholders, with each group being interviewed about one of the three forest land allocations. We used stratified sampling to divide each group of 75 respondents among several sampling locations, with a total of 23 locations for the 225 respondents. In each sampling location, respondents were selected randomly and the number of selected respondents was proportional to the total population of the location. The 23 different locations were situated inside or beside (up to 4.1 kilometers) one of the three forest allocations: (i) nine villages in the buffer zone of the protected area; (ii) four villages bordering the logging concession, the workers' camp, and the headquarters of the company; and (iii) eight villages located inside the three community forests (Figure 3.1). These locations covered more than 50% of all possible survey locations.

The total sample size of 225 was based on an estimation of the minimal number of respondents needed (n) to reach a statistical accuracy of 5% (d) for estimating the proportion of positive answers (p) concerning each ES perception, calculated with the following formula: $n = 4\ p\ (1 - p) / d^2$ (Dagnelie, 2011). Based on the answers provided by the first 20 respondents interviewed (p), we estimated the total sample size needed (n) to reach the statistical accuracy of 5% (d) for estimating the proportion of positive answers for each individual ES perception. We used the minimum value obtained to define our real sample size of 225 respondents. Based on the final dataset of individual ES perceptions (p), we confirmed that the sample size of 225 respondents (n) was sufficient to reach a statistical accuracy of 5% (d).

3.3. Questionnaire survey

In order to evaluate the ES perceptions of forest stakeholders, we used a questionnaire survey conducted face to face with the 225 respondents. The questionnaire survey was conducted on a voluntary basis after the investigator explained the aim of the study with a systematic statement. Respondents gave their free, prior, and informed verbal consent for participation. Our methodology followed the recommendations of Bird (2009). Three groups of 75 respondents each were attributed to three distinct forest allocations. All questions were asked explicitly with respect to the forest allocation attributed to the respondent. Respondents were well aware of the limits of each forest allocation and these limits are clearly and physically materialized with painted trees and well-maintained paths. The questionnaire survey was divided into two sections to collect information about two distinct types of ES perceptions (Table 3.1): First, a general, open-ended question was asked to identify the spontaneous perceptions of ES significance: 'What are the usefulness and interests of this forest for local populations?' Second, 16 directed questions allowed evaluation of the perceptions of ES abundance for 16 particular ES. Respondents were encouraged to justify their answers with a short explanation. The 16 ES were grouped into provisioning ES, regulating ES, and cultural &

amenity ES according to the standard classification of The Economics of Ecosystems and Biodiversity (R.S. de Groot *et al.*, 2010). The 16 questions were asked in random order to avoid any influence among provisioning, regulating, and cultural & amenity ES perceptions. Selection of the 16 ES included in the directed questions was based on a combination of different lists of ES provided by tropical forests (Brandon, 2014; de Groot *et al.*, 2002; Fenton, 2012). The term ‘ecosystem services’ was not explicitly used during the survey, but rather the concrete benefits that people directly get from forests were mentioned (Orenstein and Groner, 2014). The questionnaire was tested with 10 local experts (scientists and officials) before conducting the survey.

The questionnaire survey was carried out by the same investigator between March and May 2016. Questions and answers were in French for 210 respondents (one of the two national official languages of Cameroon, the other being English) and with the assistance of a translator in the Baka language for 15 respondents. The investigator was trained to conduct and deliver the questionnaire to avoid any differences in data collection, as recommended by Collins (2003). Individual surveys lasted between 15 and 45 minutes. The investigator took notes and did not use any recorder. If our methodology was scaled up with more respondents and several investigators, use of audio recording instead of note-taking would have been recommended to avoid any bias between investigators, as well as a unique translator if possible.

Table 3.1: Classification questions asked to the 225 respondents and the two-section questionnaire survey used for the evaluation of ecosystem services (ES) perceptions. (A) The first section of the questionnaire was a general open-ended question for the evaluation of ES significance, and (B) the second section comprised 16 directed questions for evaluating the perceptions of ES abundance, corresponding to a set of 16 ES provided by tropical forests and grouped into: provisioning ES (n = 6), regulating ES (n = 5), and cultural & amenity ES (n = 5). The service 'Vegetal NTFP' gathers the provision of all vegetal non-timber forest products coming from the forest (wild fruits, leaves, tubers, mushrooms, raw materials, etc.), except traditional medicine which has been evaluated separately.

Classification questions:		
	Gender?	
	Age?	
	Ethnicity?	
	Main occupation?	
A) Open-ended question (perceptions of ES significance):		
	"What are the usefulness and interests of this forest for local populations?"	
B) Directed questions (perceptions of ES abundance):		
Categories of ES	**Ecosystem services**	**Questions ("Yes/No? Please explain…")**
Provisioning ES (n = 6)	Meat (hunting)	"Is there a lot of meat coming from hunting in this forest?"
	Fish (fishing)	"Is there a lot of fish coming from fishing in this forest?"
	Vegetal NTFP	"Are there a lot of vegetal non-timber forest products coming from gathering in this forest?"
	Traditional medicine	"Is there a lot of traditional medicine coming from this forest?"
	Timber	"Do local populations find a lot of timber coming from this forest?"
	Firewood	"Do local populations find a lot of firewood coming from this forest?"
Regulating ES (n = 5)	Climate regulation	"Does this forest influence the climate? If all of this forest is cut, would the climate and seasons be different?"
	Water quality regulation	"Is the water quality better in the rivers of this forest than outside?"
	Air quality regulation	"Is the air quality better in this forest than outside?"
	Soil formation and regeneration	"Is the soil fertility better in this forest than outside for slash-and-burn practices?"
	Natural hazard mitigation	"Does this forest protect the population against disturbances, as storms, floods or diseases?"
Cultural & amenity ES (n = 5)	Cultural heritage and identity	"Is this forest part of the heritage of local populations? Does it have a symbolic value?"
	Inspiration for culture	"Is it possible to see many plants, trees, animals, and insects in this forest?"
	Spiritual experience	"Are there a lot of rituals and traditions in this forest?"
	Recreation	"Do local populations sometimes go inside this forest to relax and stroll without working?"
	Tourism	"Are there a lot of tourists coming in this forest and paying something to come?"

3.4. Data analysis

The answers obtained from the two sections of the questionnaire survey (one open-ended question and 16 directed questions) were considered as two independent datasets coded in binary values. They were office-coded from the week after the last questionnaire conducted (Bird, 2009). A list of all forest ES identified in the open-ended answers (first section of the questionnaire, perceptions of ES significance) was compiled. The open-ended answer of each respondent was then coded as a list of binary values: we attributed the value ‘1’ to each ES identified in the answer of the respondent, and the value ‘0’ to each ES not identified. Answers to the 16 directed questions (second section of the questionnaire, perceptions of ES abundance) were also coded as 16 binary values: ‘0’ values were attributed to ES perceived as ‘not provided’ or ‘less provided than before’, and ‘1’ values were attributed to ES perceived as ‘clearly provided’.

The most frequently reported ES provided by forests to local populations were identified using both answer datasets (R package ‘ggplot2’, Wickam, 2009). In each of the two datasets, we calculated the proportions of respondents identifying each ES individually, and identifying at least one ES out of the three ES categories (provisioning, regulating, and cultural & amenity ES).

In order to identify the effect of spatial and socio-demographic variables as potential determinants of the perceptions of ES abundance, we used 16 logistic regressions modelling the probability of positive answers for each individual ES (second section of the questionnaire) as a function of the six following variables: (i) the forest allocation considered in the answers (spatial qualitative variable), (ii) the deforestation rate between 2000 and 2012 around the sampling locations (spatial quantitative variable), (iii) gender (socio-demographic qualitative variable), (iv) age (socio-demographic quantitative variable), (v) ethnicity (socio-demographic qualitative variable), and (vi) the main occupation of each respondent (socio-demographic qualitative variable). *P*-values were adjusted with the Benjamini and Hochberg (1995) method to account for multiple comparisons, controlling the false discovery rate. For each significant qualitative variable explaining the perception of a service, we computed confidence intervals on the differences among the means of levels of the variable with Tukey’s ‘Honest Significant Differences’ method (level of significance: $P < 0.05$), based on an analysis of variance model. For each significant quantitative variable (deforestation rate and age of respondents) explaining the perception of a service, we confirmed their significance in shaping the ES perceptions with Pearson’s correlation tests.

The deforestation rate (Figure 3.1C) used in the previous analysis was calculated in a circle of radius 2 kilometers centered on each sampling location, using the 30-meters spatial resolution data of net tree cover loss between 2000 and 2012 (Hansen *et al.*, 2013). The calculated deforestation rates around the sampling locations were used to quantify the impacts of the direct surrounding environment of the respondents on their perceptions of ES, more than the deforestation in overall forest allocations. We chose a radius of 2 kilometers for calculating the deforestation rates in order to avoid overlaps of calculated deforestation between adjacent sampling locations, and based on the mean distance of 2.2 kilometers to access the collection sites of NTFPs from the center of the largest village in the study area (Gillet *et al.*, 2016a). Mertens and Lambin (1997) also observed that more than 80% of all deforestation occurred at a distance less than 2.5 kilometers from main roads in southern Cameroon.

4. Results and Discussion

4.1. Characteristics of respondents

Despite our random sampling, more men (78% of respondents) were interviewed because women were less willing to participate when asked to. Indeed, as in many traditional African societies, household heads are usually men, which potentially affects the willingness for women to express their opinion (Dave *et al.*, 2016). However, the sex ratio of respondents was similar among the three forest allocations. Respondents were between 15 and 79 years old, the mean age was 43. Respondents were divided into six ethnolinguistic groups: Badjoué (43% of respondents), Nzimé (18%), Ndjem (3%), Baka Pygmy (7%), non-local Cameroonians (25%), and foreigners (4%, only corresponding to expatriates working in the logging concession). The main occupations of the respondents were: farmers (37% of respondents), salaried (29%), mixed occupation (19%, comprising respondents who acknowledged having more than one occupation), students (6%), officials (4%), fishermen (1%), hunters (1%), and others (3%, comprising merchants, tour guides, and taxi men). The characteristics of the 225 respondents match the socio-economic surveys conducted by the logging concession (Cellule Aménagement Pallisco and Nature+, 2015), and the respondents can be considered as representative of local communities and forest stakeholders in the study area. Additional details about the sampled population are provided in Appendix 6.

4.2. Perceptions of ES significance and abundance

We compiled a list of 17 ES mentioned in the open-ended answers (first section of the questionnaire, perceptions of ES significance). Only three differences were observed with the list of 16 ES used in the directed questions (second section of the questionnaire, perceptions of ES abundance): firewood and timber were combined as ‘wood’, and two supplementary cultural ES were identified (education and housing). When analyzing the ES reported most frequently, spontaneous (ES significance) and directed perceptions (ES abundance) showed different results (Figure 3.2).

Perceptions of ES significance mainly comprised provisioning (93.3% of respondents) and cultural & amenity (68.0%) ES (spontaneous perceptions, Figure 3.2A). In contrast, regulating services were much less frequently mentioned (16.0%), and were almost exclusively mentioned in the protected area (33.3% of respondents from the protected area, 10.7% from the logging concession, and 4.0% from the community forests). This result highlights the influence of past awareness campaigns on spontaneous ES perceptions, as also shown by other authors (*e.g.*, Hartter and Goldman (2011) in Uganda). This supports the possible appropriation of future conservation programs by local populations based on environmental education (Caballero-Serrano *et al.*, 2017), raising awareness of the benefits and provision of ES (Bryan *et al.*, 2010), and explanation of the law (Vermeulen *et al.*, 2009). In the protected area, 93.3% of respondents identified at least one cultural & amenity ES, compared to 57.3% in the community forests and 53.3% in the logging concession. The most frequently perceived ES were: vegetal non-timber forest products provision (83.6% of all respondents), meat provision (59.6%), cultural heritage (50.2%), fish provision (36.0%), wood provision (34.7%), and traditional medicine provision (30.2%).

Provisioning services were also the most frequently perceived ES in other studies such as Hartter (2010) in Uganda, Zhang *et al.* (2016) in Nigeria, or Dave *et al.* (2016) in Madagascar. The perceptions of provisioning services from the forest were also analyzed by Sassen and Jum (2007) in central Cameroon, who showed high dependency of farmers on the forest for their livelihoods. In a subsistence economy based on the primary sector, particularly in developing countries, provisioning services are considered as the most important (Iftekhar and Takama, 2007), associated with more tangible and identifiable value (Rodríguez *et al.*, 2006), and being fundamental for the livelihoods of local populations (Fagerholm *et al.*, 2012). Therefore, provisioning ES are also more frequently assessed than other categories (*e.g.*, Guerbois and Fritz (2017) in Zimbabwe). But, our results also show that forest stakeholders were aware of the abundant supply of all regulating ES when explicitly questioned about them using directed questions.

All respondents identified the abundance of at least one provisioning and one regulating ES, and in most cases (99.6%), at least one cultural & amenity ES as well (directed perceptions, Figure 3.2B). The abundant ES most frequently identified from the 16 directed questions were: provision of traditional medicine (97.3% of all respondents), cultural heritage (96.9%), provision of vegetal non-timber forest products (96.4%), natural hazard mitigation (93.3%), air quality regulation (85.3%), climate regulation (83.6%), fish provision (82.2%), soil formation and regeneration (82.2%), water quality regulation (76.0%), spiritual experience (75.1%), firewood provision (71.6%), and inspiration for culture (69.3%).

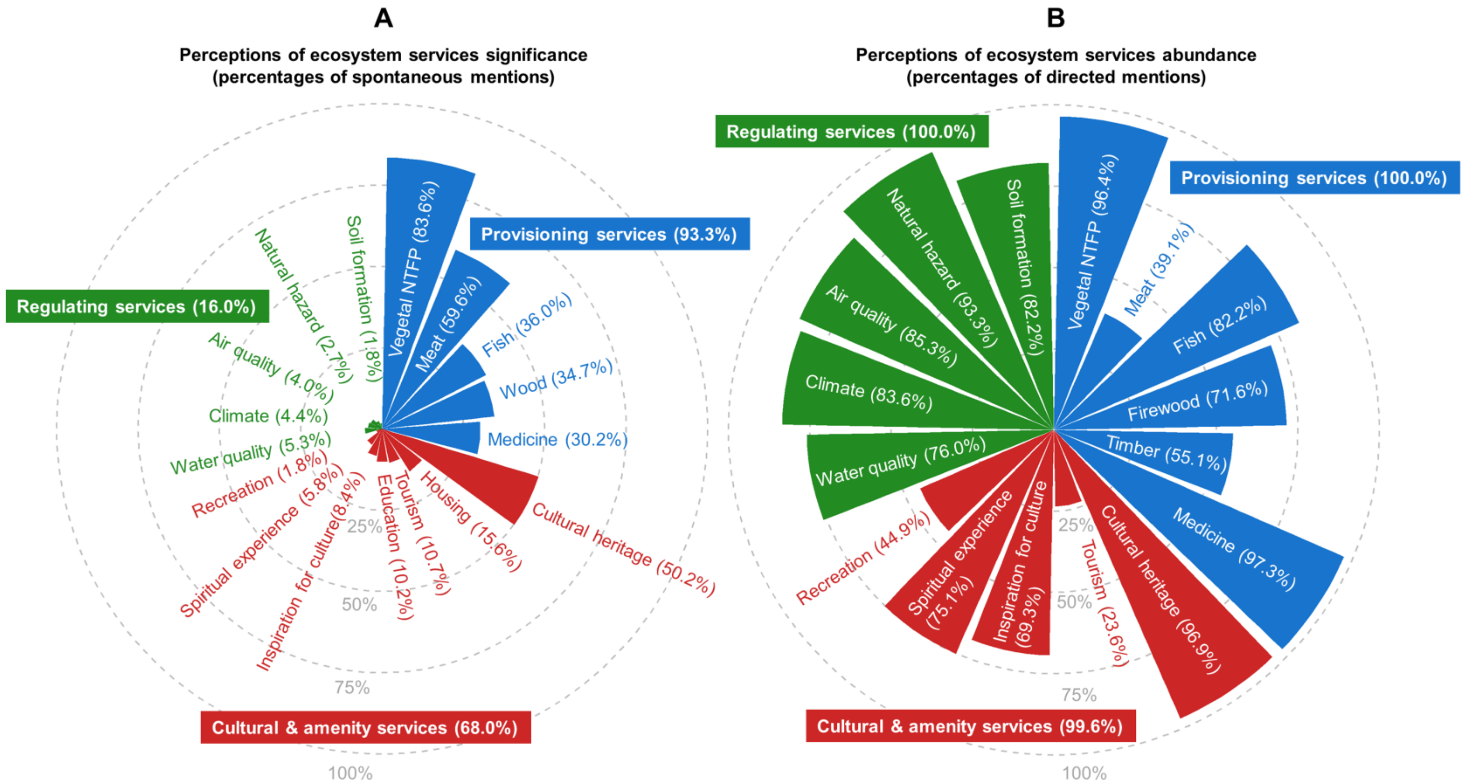


Figure 3.2: Percentages of 17 spontaneous (A, ES significance) and 16 directed (B, ES abundance) perceptions of forest ecosystem services from interviewing 225 forest stakeholders. Percentages for each individual ES show the proportion of all respondents mentioning these ES. Percentages in boxes are the proportions of respondents mentioning at least one ES in each of the three ES categories. Three differences have to be noticed in the list of spontaneous perceptions (A) in comparison with the list of directed perceptions (B): firewood and timber were combined as ‘wood’, and two supplementary cultural & amenity ES were identified (education and housing).

The existing scientific literature is not unanimous concerning the interpretation of relative frequencies of perceptions on provisioning, regulating, and cultural ES. Some authors argue that rural populations perceive provisioning ES more frequently than in urban societies, due to a cognitive disconnection of human well-being from life supporting environments in cities (*e.g.*, Casado-Arzuaga *et al.*, 2013; Martín-López *et al.*, 2012). Others emphasize that rural residents mention regulating and cultural ES more frequently than provisioning ES, because they possess ecological knowledge of the importance of the environment and the forests' ES (*e.g.*, Muhamad *et al.*, 2014). Our results showed that, depending on the method used (evaluation of spontaneous or directed perceptions), both these hypotheses could be confirmed.

Logically, perceptions of ES abundance included more frequent mentions of all individual ES than spontaneous ES significance, with the exception of meat provision. This implies that according to forest stakeholders' perceptions, meat abundance could not be sufficient to meet its high significance for local populations. However, the perceptions of meat significance and abundance must be interpreted critically and are most probably underestimated. Indeed, hunting practices are prohibited or at least regulated in the three forest allocations (see Appendix 1), potentially leading to false answers of respondents wanting to conceal their knowledge of hunting practices, particularly in the protected area and the logging concession. Respondents were possibly inhibited by the fear of controls and repression by the investigator, despite being an independent researcher. Gillet *et al.* (2016) noticed particularly high hunting pressure in this area. Hunting practices target a wide range of animal species, of varying sizes from large mammals to very small rodents in highly defaunated areas. Commercial hunting has also been recognized as a major threat in the Dja Reserve (Betti, 2004), and the conservation effectiveness of this protected area has been questioned. Moreover, accessible forests such as community forests are known to be strongly defaunated and can be considered as 'empty forests' (Nasi *et al.*, 2011), thus inducing major ecological consequences.

4.3. Determinants of perceptions of ES abundance

Slight variations in the perceptions of ES abundance were identified. Nevertheless, we used logistic regressions to identify their spatial or social determinants. The two spatial variables 'forest land allocation' and 'deforestation rate' significantly influenced the perceptions of the abundance of five and two individual ES. The four socio-demographic variables had fewer impacts (Table 3.2): 'gender,' 'age,' 'ethnicity,' and 'main occupation' each significantly influenced the perceptions of one individual ES. Prior to this analysis, we removed two categories of 'main occupation' from the dataset as they were each only represented by two respondents ('fishermen' and 'hunters'). The adjusted *P*-values associated with the explanatory variables of 16 logistic regressions are provided in Appendix 7.

Perceptions of the five ES abundances significantly influenced by forest allocation were firewood, tourism, inspiration for culture, timber, and spiritual experience in decreasing order of significance. The protected area showed the most frequent mentions of two ES: inspiration for culture and tourism. The logging concession showed the most frequent mentions of one ES: spiritual experience (linked to the respect that local populations maintain for ancient villages mainly situated in the logging concession far from main roads and considered as sacred sites). The community forests showed the most frequent mentions of two ES: firewood and timber provision. Apart from these particular ES, perceptions of individual ES abundance did not differ among the three studied forest allocations. This implies that these forests present rather similar potentials in their ES supply, which is also explained by comparable forest covers: from 89.5% in the buffer zone of the protected area to 90.9% in the agroforestry zone of the logging concession (Appendix 1). We could then expect to observe more distinct differences in the perceptions of ES abundance in comparison with other land uses, such as mining concessions or agricultural areas. The respondents from areas that experienced the highest deforestation rates between 2000 and 2012 perceived the abundance of timber and firewood less frequently (58 respondents were interviewed in areas with more than 5% of deforestation). The net deforestation rates for the period 2000-2012 in a radius of 2 kilometers from the sampling locations were between 0.0% and 12.7% (Hansen *et al.*, 2013), with the following means for sampling locations grouped by forest allocations: 0.5% for the protected area, 5.0% for the logging concession, and 3.1% for the community forests. The net deforestation rates estimated in close vicinity (2 kilometers) of the respondents were independent of the net deforestation rates inside each whole forest allocation, which were: 0.0% in the protected area (core area), 0.1% in the logging concession, and 1.5% in the community forests for the same period (see Appendix 1 for more details). Several authors have already shown the influence of spatial variables in shaping ES perceptions, highlighting the role of the interview location (Cuni-Sanchez *et al.*, 2016; Hartter *et al.*, 2014), local landscape (Alassaf *et al.*, 2014; Allendorf and Yang, 2013; Muhamad *et al.*, 2014; Zhang *et al.*, 2016), vicinity and access to forest resources (Castillo *et al.*, 2005; Diaz *et al.*, 2011; Sodhi *et al.*, 2010), and the use (or non-use) of particular areas in the landscape (Alassaf *et al.*, 2014; Allendorf and Yang, 2013; Muhamad *et al.*, 2014).

Women perceived the abundance of timber more frequently than men. The cultural inspiration from the forest was less frequent for older respondents. Cultural inspiration was evaluated with a question about the diversity of visible species in the forest (Osawa *et al.*, 2020), suggesting that older respondents currently perceive the existence of less species in forests than in the past. The ethnicity of the respondents significantly explained the perceptions of water quality regulation: Badjoué respondents mentioned the role of the forest in water quality regulation more frequently than the Nzimé and non-native Cameroonian respondents. Respondents with different occupations showed distinct perceptions of the supply of bushmeat through hunting: salaried and students perceived a high abundance of meat more frequently than the officials and respondents with mixed occupations. Socio-demographic variables were only rarely observed as determinants of ES perceptions in our study in southeastern Cameroon, in contrast with other studies. For example, socioeconomic status (Alassaf *et al.*, 2014; Allendorf and Yang, 2013; Caballero-Serrano *et al.*, 2017; Hartter *et al.*, 2014; Muhamad *et al.*, 2014; Orenstein and Groner, 2014), education level (Allendorf and Yang, 2013; Sodhi *et al.*, 2010), age (Allendorf and Yang, 2013; Martín-López *et al.*, 2012), gender (Allendorf and Yang, 2013; Hartter, 2010; Orenstein and Groner, 2014; Rönnbäck *et al.*, 2007; Warren-Rhodes *et al.*, 2011), social conditioning (Zhang *et al.*, 2016), life experience and historic relationships with the environment (Alassaf *et al.*, 2014; Allendorf and Yang, 2013; Caballero-Serrano *et al.*, 2017; Muhamad *et al.*, 2014; Zhang *et al.*, 2016) were highlighted as important determinants of ES perceptions in other contexts. The importance of certain socio-demographic variables as determinants of ES perceptions in other studies clearly shows that ES perceptions are highly dependent on the local socio-cultural context (Alassaf *et al.*, 2014; Allendorf and Yang, 2013; Caballero-Serrano *et al.*, 2017; Hartter *et al.*, 2014; Muhamad *et al.*, 2014; Orenstein and Groner, 2014), notably defined by land tenure and village territory size in Central Africa (Gillet *et al.*, 2016a, 2015).

The perceptions of the abundance of nine ES (out of 16) were not explained by any of the six spatial or socio-demographic variables (Table 3.2). Our hypothesis of variations in ES abundance among contrasting forest allocations led us to conduct a spatial stratified sampling. Although our results showed relative homogeneity of ES perceptions through the area, it is still difficult to disentangle the major effects between social and spatial determinants because of unbalanced social sampling (see Appendix 6).

Table 3.2: Influence of explanatory variables (forest allocation, deforestation rate, gender, age, ethnicity, and main occupation) on the perceptions of ecosystem services abundance, according to 16 logistic regressions, Tukey's tests for qualitative variables, and correlation tests for quantitative variables. For significant qualitative variables in columns (forest allocation, gender, ethnicity and main occupation), we provide the proportions of positive answers obtained for the perceptions of the ES in line and the letters in parentheses summarize the similarities and differences among levels according to Tukey's tests. For quantitative variables (deforestation and age), a significant decrease in the perception of ES abundance with the increasing variable is indicated with ↓. Indication 'n.s.' stands for 'not significant' influence of the variable in the column on ES perceptions in line.

	Land allocation type				Gender			Ethnicity						Main occupation					
Services	Protected area	Logging concession	Community forests	Deforestation	Man	Woman	Age	Badjoué	Nzimé	Ndjem	Baka	Other Cameroonian	Foreigner	Farmer	Salaried	Mixed	Official	Student	Other
Vegetal NTFP	n.s.			n.s.	n.s.		n.s.	n.s.						n.s.					
Meat (hunting)	n.s.			n.s.	n.s.		n.s.	n.s.						36% (ab)	52% (b)	16% (a)	0% (a)	69% (b)	67% (ab)
Fish (fishing)	n.s.			n.s.	n.s.		n.s.	n.s.						n.s.					
Firewood	52% (a)	61% (a)	100% (b)	↓	n.s.		n.s.	n.s.						n.s.					
Timber	53% (ab)	43% (a)	67% (b)	↓	49% (a)	74% (b)	n.s.	n.s.						n.s.					
Traditional medicine	n.s.			n.s.	n.s.		n.s.	n.s.						n.s.					
Cultural heritage and identity	n.s.			n.s.	n.s.		n.s.	n.s.						n.s.					
Tourism	64% (b)	1% (a)	5% (a)	n.s.	n.s.		n.s.	n.s.						n.s.					
Inspiration for culture	93% (c)	71% (b)	44% (a)	n.s.	n.s.		↓	n.s.						n.s.					
Spiritual experience	78% (ab)	84% (b)	63% (a)	n.s.	n.s.		n.s.	n.s.						n.s.					
Recreation	n.s.			n.s.	n.s.		n.s.	n.s.						n.s.					
Water quality regulation	n.s.			n.s.	n.s.		n.s.	88% (b)	58% (a)	50% (ab)	93% (ab)	68% (a)	60% (ab)	n.s.					
Climate regulation	n.s.			n.s.	n.s.		n.s.	n.s.						n.s.					
Air quality regulation	n.s.			n.s.	n.s.		n.s.	n.s.						n.s.					
Natural hazard mitigation	n.s.			n.s.	n.s.		n.s.	n.s.						n.s.					
Soil formation and regeneration	n.s.			n.s.	n.s.		n.s.	n.s.						n.s.					

4.4. Need for an integrated ES assessment

While ES have already been investigated in other regions of Africa (*e.g.*, Byg *et al.*, 2017; Dawson and Martin, 2015; Hartter and Goldman, 2011), our study was the first step in integrated local-scale assessment of multiple ES provided by forests in Central Africa. We used a social approach to consider the perceptions of ES significance and abundance before implementing the more frequent ecological and economic approaches (Boeraeve et al., 2015; Cuni-Sanchez et al., 2016; Kremen and Ostfeld, 2005; Martín-López et al., 2014; Satz et al., 2013; Spangenberg and Settele, 2010).

The local forest stakeholders must inevitably be integrated in ES assessments as they are daily using, managing, and changing these ecosystems (Muhamad *et al.*, 2014). A social approach in ES assessment could not be replaced by a unique economic valuation. Indeed, monetary proxies overlook the non-material benefits provided by ecosystems (Dawson and Martin, 2015). These benefits can be the basis for interpreting the ES perceptions obtained from social approaches, such as considering the importance of spiritual experience in the logging concession in our study.

As a priority, we recommend gaining further insights on the unique ES for which the perceptions of abundance do not meet the ES significance, *i.e.*, bushmeat provision. This is essential for any policy ambitions for the maintenance of ES supply and sustainable management (Geijzendorffer and Roche, 2014). We also propose to quantify the most variable (and controversial) ES in terms of perceptions of abundance such as recreation, tourism, timber provision, spiritual experience, firewood provision, meat provision, water quality regulation, and inspiration for culture (species richness), using complementary assessment methods. The supply of all of these ES should be quantified with detailed monitoring, integrating spatial and temporal variability, using market surveys for provisioning ES (Levang *et al.*, 2015), social mapping for cultural ES (Fagerholm *et al.*, 2012), and ecological measures for regulating ES (Mononen *et al.*, 2017).

Our study could be replicated and integrated at a larger scale across Central African forests and countries. We acknowledge that no one should directly extrapolate our results to the entire Central African region or even to other communities. Although only slight variations were observed among ES perceptions in contrasting forest allocations, over-simplifying complex socio-ecosystems across large scales could lead to a lack of policy relevance of interpretations and decisions. Local studies of people's uses and preferences are essential for a proper understanding of social-ecological systems (Dawson and Martin, 2015). Qualitative assessments of ES provision are also required to implement sustainable management strategies and decisions (Braat and de Groot, 2012; Collins *et al.*, 2010).

4.5. Practical implications for management

We indicate three concrete recommendations for forest management based on our results.

First, bushmeat provision appeared to be the most deficient in the perceptions of ES abundance, compared to ES significance. In Central Africa, both biodiversity conservation and human food security must be pursued through multiple compatible interventions (Friant *et al.*, 2015; Lindsey *et al.*, 2013). Law enforcement is indispensable to mitigate illegal poaching (Critchlow *et al.*, 2017; Lindsey *et al.*, 2013) but a complete ban is not conceivable for poor households heavily dependent on bushmeat as their main source of proteins (Challender and MacMillan, 2014; Foerster *et al.*, 2012; Lindsey *et al.*, 2013). We suggest implementing participatory repressive enforcement program in the logging concession, targeting the poaching businesses with the participation of local populations (Vermeulen *et al.*, 2009). We also highlight the importance of distinguishing endangered species (such as great apes) that must not be hunted, and more resilient species, such as the blue duiker (*Philantomba monticola*) or the African brush-tailed porcupine (*Atherurus africanus*), that could sustain moderate hunting pressure (Nasi *et al.*, 2011; van Vliet and Nasi, 2008). Even if factors such as taste preference or tradition may influence human dietary choices (Ordaz-Németh *et al.*, 2017), we also recommend providing alternative sources of proteins, for instance through local fish farming, local aviculture, or supply of butcher's meat in a small grocery equipped with a freezer. Any adequate domestic fishery or animal rearing system needs to minimize negative environmental impacts (Lindsey *et al.*, 2013; Rentsch and Damon, 2013; Wilkie *et al.*, 2005), and offer products at affordable prices for poor rural populations. Cultural appropriation of alternative sources of proteins could also be critical, considering the mental blocks for rearing activities in Central Africa. Use of vegetal proteins such as beans and other pulses (Ordaz-Németh *et al.*, 2017), and edible insects (particularly caterpillars) that are highly consumed in Cameroon (Meutchieye *et al.*, 2016) should also be considered and expanded as alternative sources of proteins.

Second, considering the perceptions of high abundance of NTFP (96.4% of respondents), this economic sector shows a high potential as an alternative livelihood for the future. In Cameroon, NTFP are an important source of food (Sassen and Jum, 2007) and income for households (Lescuyer, 2010). Domestication of NTFP species for agroforestry systems have shown potential to improve livelihoods (Ingram et al., 2012; Vermeulen and Fankap, 2001). Endamana *et al.* (2016) identified the following NTFP as the most important sources of cash income in Cameroon, Congo, and the Central African Republic: honey, medicinal plants, okok (*Gnetum africanum*), bush mangoes (*Irvingia* ssp.), cola nuts (*Cola* spp.), palm wine and mats (*Raphia* spp., *Elaeis guineensis*), caterpillars, mushrooms, and arrowroot (Marantaceae) leaves.

Third, knowing the current fragility of the forest sector in the region, specifically FSC-certified companies (Karsenty, 2018), we promote the new model of

'Concessions 2.0' adapted to the future challenges of Central African forests (Karsenty and Vermeulen, 2016). This model suggests a shift from the classic logging concession system solely involving the state and the private sector for wood exploitation. It moves towards a new model of governance based on a multi-stakeholder platform (including local populations and local NGOs) empowered to make decisions on the management and marketing of other resources (comprising NTFP) inside the concession. Considering the differences of perceptions of ES abundance among forest allocations for wood and cultural ES, including tourism (Table 3.2), this model could answer various needs of local populations. Concessions 2.0 would allow associative or commercial valorization of many ES; it combines the mapping and recognition of customary territories inside and around the logging concession, sharing of timber resources and revenue, commercial exploitation of NTFP, and management of overlapping rights through inclusive governance. A better inclusion of all user rights of local populations in the management strategy of the logging concession could avoid major conflicts such as superposition of agricultural and logging activities, severe poaching, and illegal logging (Levang *et al.*, 2015). Concessions 2.0 also constitute an opportunity to develop tourism for the benefit of local communities, with the possible support of another economic operator. To our knowledge, no logging concession in Central Africa is involved in the development of eco-tourism. Tourism ES was perceived by respondents as the least abundant, but there is an eco-tourism potential in the three forest allocations, which is slightly exploited only in the protected area. The practical challenges to be overcome include facilitating procedures to obtain visas at the national level, and developing visitor facilities and infrastructure (transport and accommodation) at the local level.

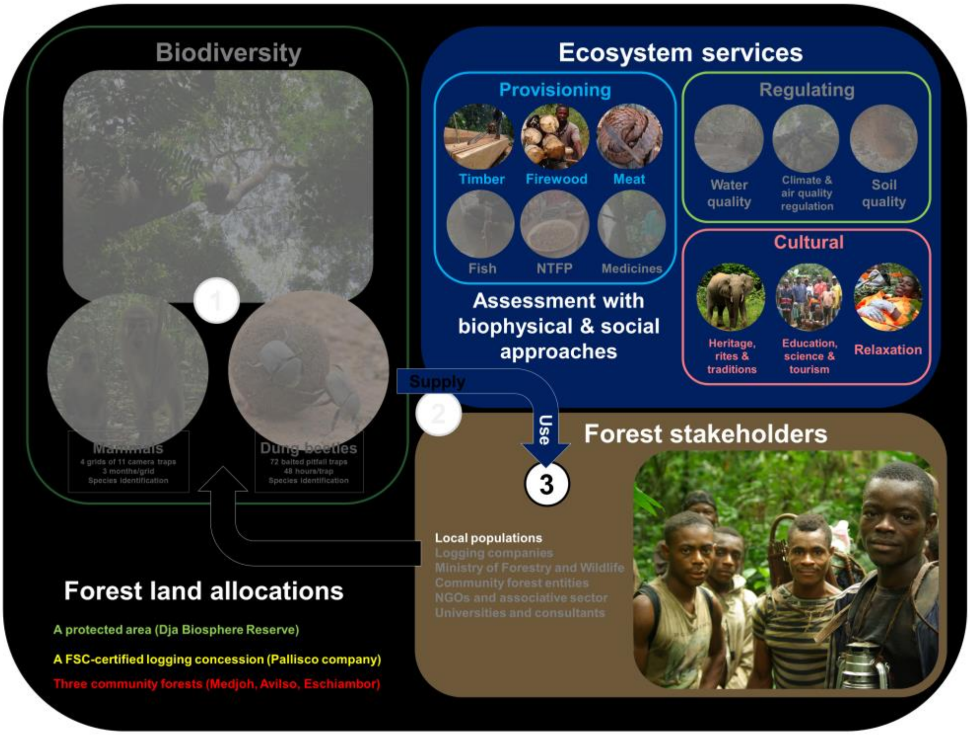
5. Conclusions

In this study, we integrated all ecosystem services (ES) that are classically attributed to tropical forests in the first social assessment of ES significance and abundance for local populations in southeastern Cameroon. Our results highlighted a high significance of provisioning and cultural & amenity ES. The perceptions of the abundance of all ES met the ES significance except for bushmeat provision. We identified only slight variations in the perceptions of ES abundance, revealing relative homogeneity and similar ES perceptions among different forest allocations and respondents. We proposed eight ES to be quantified with complementary ecological and economic methods, and three concrete recommendations for forest management.

4

Use of forest ecosystem services by local populations

1. Preamble



In this chapter, we aimed to depict the use of ecosystem services provided by tropical forests to local populations in southeastern Cameroon, identify its determinants and evaluate its sustainability. Field surveys (biophysical approaches) and various interviews (social approaches) were conducted in three villages, focusing on three provisioning services (bushmeat, firewood, and timber), and five cultural services (cultural heritage, inspiration, spiritual experience, recreation, and education).

This chapter is adapted from: Lhoest S., Vermeulen C., Fayolle A., Jamar P., Hette S., Nkodo A., Maréchal K., Dufrêne M. & Meyfroidt P. (2020). Quantifying the use of forest ecosystem services by local populations in southeastern Cameroon. *Sustainability*, 12(6), 2505.

2. Introduction

The importance and extent of human impacts on the global environment have led to the recognition of the new Anthropocene era (Lewis and Maslin, 2015). In the face of the largest environmental and biodiversity crisis, being recognized as the sixth extinction period (Ceballos *et al.*, 2015), the importance of ecological systems to human societies has been raised, and the concept of ecosystem services (ES) emerged (Millennium Ecosystem Assessment, 2005). ES are defined as the contributions of ecosystems to human well-being (Burkhard *et al.*, 2012). Classically, ES are divided into provisioning, regulating, and cultural services (R.S. de Groot *et al.*, 2010), provisioning and cultural services being directly and daily used by people depending on the forests, especially in developing countries (Fagerholm *et al.*, 2012; Lhoest *et al.*, 2019).

The Congo basin forests, which represent the second largest block of continuous tropical forests worldwide after the Amazon, provide important contributions to the rural livelihoods of more than 60 million people (de Wasseige *et al.*, 2015). With the exception of the surroundings of big cities (Abernethy *et al.*, 2016) and roads (Kleinschroth *et al.*, 2019), the Congo basin can be considered as a relatively preserved area with only little deforestation in comparison to the other tropical regions (Achard *et al.*, 2014). However, Central African forests are exposed to increasing human pressures, including population growth, climate change, overexploitation, and weak governance (Abernethy *et al.*, 2016). These pressures are susceptible to influence the capacity of forest ecosystems to provide ES to local populations (Igu and Marchant, 2017), raising potential sustainability issues.

Provisioning services provided by tropical forests to local populations in Central Africa include wild food (bushmeat, fish, fruit, mushrooms, and caterpillars), water, raw materials (timber, fibers, and firewood), and traditional medicinal resources (Egoh *et al.*, 2012). Among the different non-timber forest products (NTFP) collected by local populations (comprising 500 plant and 82 animal species in Cameroon; Ingram et al., 2012), bushmeat is of major importance. Bushmeat hunting is estimated between 4.6 and 4.9 million tons per year in Central Africa (Fa *et al.*, 2002; Nasi *et al.*, 2011), and it provides a significant source of proteins in the diet (Fa *et al.*, 2015). In Cameroon, the annual turnover of the bushmeat sector is estimated at € 97 million, contributing as much as the mining sector to the country's Gross Domestic Product (GDP), without even considering self-consumption of bushmeat in rural areas which may account for over € 142 million of gross annual economic benefit (Lescuyer and Nasi, 2016).

Firewood is also an important provisioning service throughout Central Africa, being the main wood resource and source of energy used by rural populations. The use of firewood and charcoal was mainly quantified in urban areas where the human pressure on natural resources is particularly strong (Sola *et al.*, 2017). Only few studies were conducted in rural forested areas (Eba'a Atyi *et al.*, 2016), where firewood is directly gathered by local populations for self-consumption to satisfy their daily needs. In Cameroon, firewood constitutes the main source of energy for 83% of households (Sola *et al.*, 2019). The total consumption of firewood in rural areas of the country is estimated at four million tons per year, corresponding to an estimated total value of € 117.4 million per year (Eba'a Atyi *et al.*, 2016).

Timber is also provided by forests, and used by rural populations for house construction (framework, posts, and joineries) and furniture. The industrial timber sector also constitutes an important part of the national Cameroonian economy, producing 2.9 million of m^3 $year^{-1}$ and contributing to 4% of the GDP: about 25% of logs are exported and about 62% of timber is transformed in the country (FRMi, 2018). The informal Cameroonian timber sector, through individual chainsaw milling, represents an estimated volume of 715 000 m^3 $year^{-1}$, with an estimated annual turnover of € 93 million (Lescuyer *et al.*, 2016). Besides these figures, significant uncertainties still remain in the quantification of the local use of these provisioning services, the sustainability and the determinants of this use, especially for self-consumption and informal markets within rural areas.

Most ES assessments in Africa solely focused on provisioning services, and cultural services have been far less studied (Wangai *et al.*, 2016). Participatory and mapping techniques are particularly useful for the assessment of cultural services, by linking social perceptions with environmental features, in any social-ecological system (Cheng *et al.*, 2019). In a review of the most important ES in Africa (Egoh *et al.*, 2012), the cultural services mentioned included natural heritage sites, the use of natural areas for rituals and spiritual worship, the use of nature for education, and tourism and leisure sites (the latter being rarer in Central Africa). In the periphery of Yaoundé, the capital of Cameroon, several cultural services were assessed using participatory approaches, including cultural heritage, landscape aesthetics, social interaction, spiritual or religious experience, and intrinsic value (Jaligot *et al.*, 2018). In southeastern Cameroon, cultural heritage and identity, inspiration for culture and art, spiritual experience, opportunities for recreation and tourism, and education were all recognized important by rural populations (Lhoest *et al.*, 2019). The management of ecosystems can influence the provision of cultural services (Jaligot *et al.*, 2018), on which human well-being directly depends (Plieninger *et al.*, 2015; Raymond *et al.*, 2013). As such, cultural services can be important motivators for managing, using, or protecting ecosystems (Chan *et al.*, 2012). In Central Africa, for instance, the Forest Stewardship Council (FSC) certification of production forests compels the logging companies to identify and respect the needs and cultural values of local communities inside forests areas allocated to production. In particular, the FSC-certified logging companies have to map and preserve the sacred sites and trees, and any important sites of cultural importance for local communities (Daïnou *et al.*, 2016).

Using integrated approaches for ES assessment is claimed as urgent and essential for better informed decisions and actions about the use of natural resources and lands, improving sustainability as well as social and environmental justice (Jacobs *et* *al.*, 2016). Integrated approaches combine biophysical, social, and economic methods (Burkhard *et al.*, 2010; Felipe-Lucia *et al.*, 2015; Jacobs *et al.*, 2016). Biophysical approaches evaluate the properties of social-ecological systems with tangible measures (Boeraeve et al., 2015; de Groot et al., 2002). Social approaches measure the values attributed by people to ES (Martín-López *et al.*, 2012). Economic approaches give monetary values to ES (Wilson and Carpenter, 1999). Each type of approaches comprises numerous methods, such as measurements of ecological characteristics for biophysical approaches, individual interviews or focus groups for social approaches, and market-based valuation tools for economic approaches. Complementarily, ES mapping constitutes a visual technique to present ES values through a biophysical, social, or economic lens (Burkhard and Maes, 2017).

ES integrated assessments are lacking globally, and particularly in forest ecosystems where ES are far less studied than in other ecosystems such as agricultural areas (Mengist and Soromessa, 2019). Most ES assessments in forests have used economic approaches (Mengist and Soromessa, 2019), whereas biophysical and social assessment methods need to be further investigated in these complex social-ecological systems. Only few studies conducted ES integrated assessment in tropical forests, for instance in southern African woodlands with the identification of human-induced processes impacting ES supply (Ryan *et al.*, 2016) and the analysis of relationships between the supply of provisioning services and environmental income of local populations (Pritchard *et al.*, 2019), or in Latin America where interdisciplinary approaches allowed providing concrete policy recommendations (Rincón-Ruiz *et al.*, 2019). In particular, none integrated ES assessment has been conducted in Central Africa, where the livelihoods of rural populations deeply rely on forest ecosystems in a context of high-poverty.

In the Dja area (Cameroon), the perceptions of ES supplied by tropical forests to local populations have been quantified among three adjacent forest allocations largely represented in Central Africa: a protected area, a logging concession, and community forests (Lhoest *et al.*, 2019). The authors recommended further investigation on the use of some ES, in particular bushmeat, for which the supply did not meet the demand, and firewood and timber provision, as well as cultural services, for which the perceptions were the most variable and controversial, and this will need complementary social and biophysical assessment approaches. Despite their importance in rural livelihoods (Gillet *et al.*, 2016a; Reyes-García *et al.*, 2019), other ES such as the gathering of some NTFP (raw materials, traditional medicine, edible insects, honey etc.) and regulating services were not considered as a high priority for integrated ES assessment. Indeed, perceptions of the supply of these ES were highly homogeneous among respondents and were then less controversial among different forest areas (Lhoest *et al.*, 2019). The identification of ES determinants is also crucial in order to design sustainable planning strategies, disentangling the roles of forest management (Nasi *et al.*, 2011; Plieninger *et al.*, 2015; Wilkie *et al.*, 2019), local environment (Hartter *et al.*, 2014; Quintas-Soriano *et al.*, 2016), and socio-demography (Carpenter *et al.*, 2006; Zhang *et al.*, 2016).

Our main objective was to quantify the use of important ES provided by tropical forests to local populations in southeastern Cameroon. Specifically, we aimed to: (i) quantify and map the use of important provisioning and cultural ES by local populations; (ii) identify the influence of potential socio-demographic determinants of ES use at the household scale; (iii) identify the influence of potential determinants of ES use at the village scale, namely total population size, forest allocations and deforestation rate; (iv) assess the sustainability of the consumption of provisioning services. Because of their importance for local populations (Lhoest *et al.*, 2019), we focused on three provisioning services (bushmeat, firewood, timber) and five cultural services (cultural heritage and identity, inspiration for culture and art, spiritual experience, recreation, and education), by combining social and biophysical assessment approaches. In order to engage local communities for the political legitimacy of assessment findings (Brondizio and Tourneau, 2016), and to promote the social inclusiveness (Brown and Weber, 2011; Jaligot *et al.*, 2018), we used participatory approaches to analyze the daily use of ES by local populations. The list of studied ES was based on the standard classification of The Economics of Ecosystems and Biodiversity – TEEB (R. S. de Groot *et al.*, 2010), considered as a follow-up of the Millennium Ecosystem Assessment for ES classification and valuation (R.S. de Groot *et al.*, 2010).

3. Material and methods

3.1. Study area

This integrated ES study was conducted in southeastern Cameroon (East Province, latitude 2°49’ – 3°44’ N, longitude 12°25’ – 14°31’ E, mean altitude of 743 meters), located in the Guineo-Congolian Region where dense forests dominate (Droissart *et al.*, 2018; White, 1983). Forests have been classified as Moist for Central Africa (Fayolle *et al.*, 2014) which corresponds to semi-deciduous forests. Mean annual temperature is 23.1°C and mean annual rainfall is 1640 mm distributed between two rainy seasons (August-November and March-June) (Hijmans *et al.*, 2005).

The East Province is the most sparsely populated of the country, with an estimated population density of 7.7 inhabitants/km² in 2015 (www.citypopulation.de) and a sparse road network. The socio-economic surveys conducted as part of the management plans of the logging concessions in this area indicated a population density of 8 inhabitants/km² (Cellule Aménagement Pallisco and Nature+, 2015). The production system of local populations is based on shifting cultivation, hunting, fishing, and gathering of forest products, in a landscape matrix where degraded secondary forests, crops and fallow areas alternate along roads (Vermeulen, 2000). Local populations comprise Baka Pygmy and Bantu people and represent between 27,000 and 30,000 inhabitants in the study area (Cellule Aménagement Pallisco and Nature+, 2015). The Baka people are the indigenous population of this area, being present before the Bantu people (Winterbottom, 1992). The Bantu people in this area correspond to the Makaa-Ndjem ethnolinguistic group (comprising Badjoué, Nzimé and Ndjem) and the A80 Zone of the Guthrie classification of languages (Guthrie, 1948).

In Cameroon, the National Forest Estate (NFE) covers 37% of the total country area (World Resources Institute, 2012) and comprises all forest areas allocated to particular uses. Three major forest allocations comprise 88% of the NFE and determine the management and use of forests: (i) protected areas (42% of the NFE), comprising core areas and buffer zones, (ii) logging concessions (40% of the NFE), comprising production, conservation, protection and agroforestry zones, and (iii) community forests (6% of the NFE). Protected areas are managed for the conservation of biodiversity and natural heritage. Logging concessions are dedicated to timber production through industrial logging and can be voluntarily certified for responsible management (such as FSC) or not. The FSC-certification engages the logging concession for the recognition of user rights of local populations, among other standards ensuring economic effectiveness, ecological integrity, and social equity (Forest Stewardship Council, 2012). The forest area allocated to FSC-certified logging concessions has however recently declined in Cameroon (Karsenty, 2019). Community forests are small forest areas centered on villages and along roads, for which the management is decentralized at the scale of rural communities (Vermeulen, 2000). User rights differ among forest allocations. In the core area of protected areas and in the protection zones of logging concessions, agriculture, artisanal logging, hunting and gathering are prohibited. Agriculture and artisanal logging are also prohibited in the production and conservation zones of logging concessions, but gathering is allowed and hunting is regulated (non-protected species can be hunted with traditional selective techniques and for self-consumption only). In the buffer zones of protected areas, in the agroforestry zones of logging concessions, and in community forests, agriculture, artisanal logging and gathering are allowed, and hunting is restricted to traditional techniques for self-consumption of non-protected species.

We selected three villages surrounded by contrasted forest allocations (Figure 4.1, Appendix 9). Malen I village is isolated inside a protected area (the Dja Biosphere Reserve) and is free of industrial logging. The Dja River can only be crossed by pirogue to penetrate inside the Reserve. Thus, no motor vehicle (apart from motorbike carried on a pirogue) can reach Malen I. The nearest town is Somalomo (~ 5,000 inhabitants) located at 21 km. Eschiambor and Mintoum villages are located within distinct community forests. Eschiambor village is located between a FSC-certified concession (Pallisco Company) and a non-certified logging concession ('Societé Industrielle de Mbang'). The nearest city of Eschiambor is Lomié (~ 19,000 inabitants), located at 16 km. Mintoum village is located between the protected area (Dja Biosphere Reserve) and the FSC-certified logging concession (Pallisco Company), on a provincial road and at a distance of 7 km from Lomié.

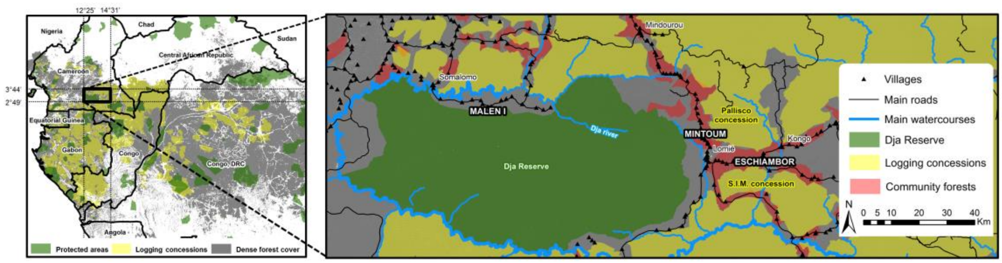


Figure 4.1: Study area and studied villages located in the Dja area (southeastern Cameroon). The 'Dense forest cover' (gray background) includes montane, submontane, lowland, and swamp forests of the land cover map of Africa (Mayaux *et al.*, 2004). We conducted our data collection for the quantification of ecosystem services use in three villages (which names are highlighted in black): Malen I (isolated in a protected area, the Dja Reserve in green), Eschiambor (located inside a community forest, in red, between a FSC-certified logging concession and a non-certified logging concession, both in yellow), and Mintoum (located inside a community forest, and between a protected area and a FSC-certified concession).

3.2. Data collection

We conducted all interviews and quantitative field surveys between March and June 2018. We systematically explained the aim of our study to local populations and all data collection was conducted on a voluntary basis, with respondents giving their free, prior, and informed verbal consent for participation in the study. We conducted interviews in French for Bantu households and with a translator for Baka households. All questionnaires were tested with 10 households sampled randomly in one village and were adjusted when needed, before conducting the interviews and surveys. Investigators were trained to conduct the interviews and surveys in order to avoid any differences in data collection (Collins, 2003). Investigators took notes and did not use a recorder. A sequence of social and biophysical methods (Figure 4.2) was used to characterize the sampled population, quantify the use of bushmeat, firewood, timber, and cultural services, to analyze the determinants of ES use at the household and at the village scale, and finally to evaluate the sustainability of the use of provisioning services.

3.2.1. Population census and sampling

No up-to-date demographic data were available for the three studied villages. Therefore, in each village, we first conducted an exhaustive population census (Appendix 9), using structured interviews with five directed questions (‘a’ in Figure 4.2): for all households, we recorded (i) the number of permanent residents (quantitative variable: defined as the household members spending the majority of their time in the village), (ii) the main source of income (four levels qualitative variable: salary jobs, agriculture, forest-related activities comprising hunting, fishing, gathering of NTFP and wood, or a mixed occupation), (iii) the ethnic group (two levels qualitative variable: Baka or Bantu), (iv) the origin (two levels qualitative variable: native from the village or not), (v) the maximum education level (four levels qualitative variable: out-of-school, primary school, secondary school, or graduate school), and we georeferenced the house.

Then, for the daily monitoring of ES use afterwards (bushmeat and firewood consumption), in each village, we sampled volunteer households (‘b’ in Figure 4.2) stratified by the main source of income (salary/agriculture/forest) and by the ethnic group (Baka or Bantu) (Gillet *et al.*, 2016a; Wollenberg and Ingles, 1998). We sampled a total of 55 households (16 in Malen I, 19 in Eschiambor, and 20 in Mintoum, corresponding respectively to 100%, 49%, and 26% of the total number of households in each village).

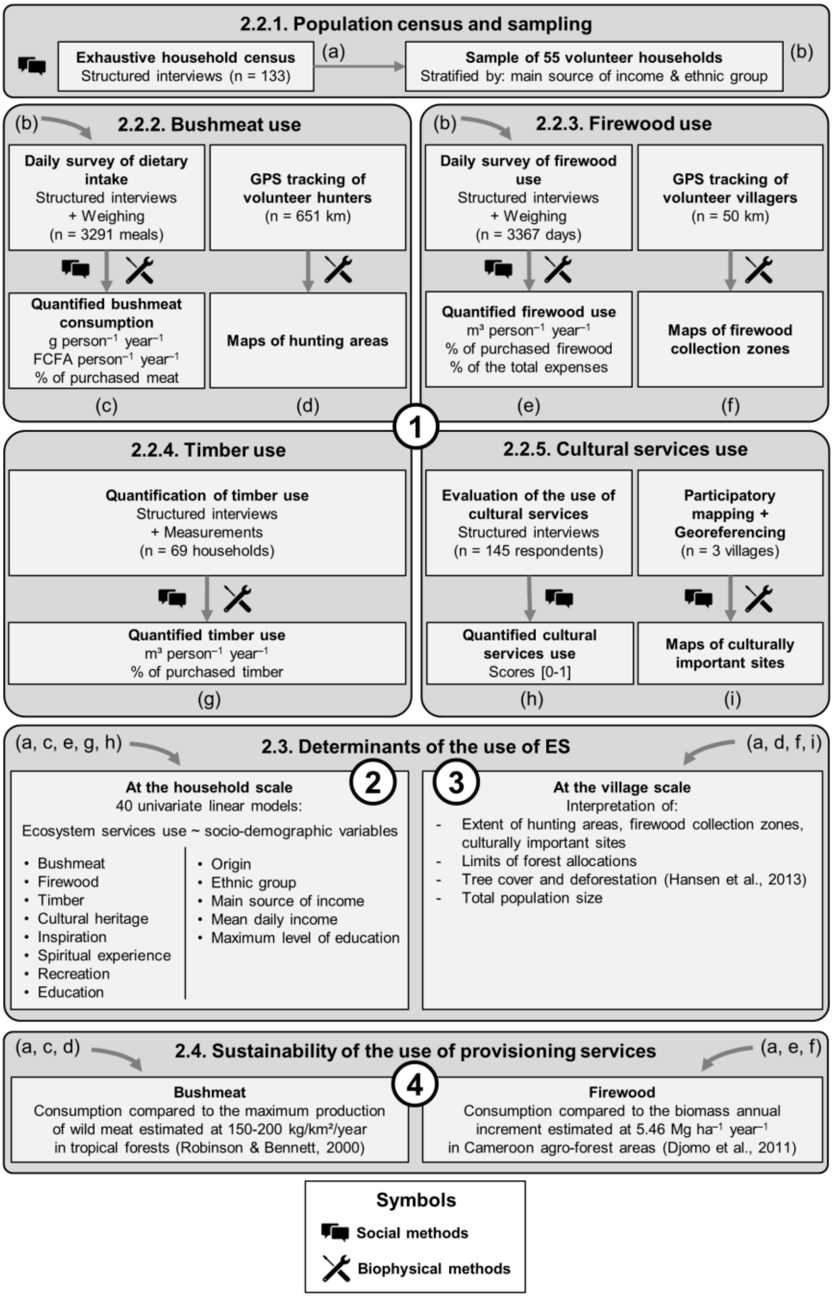


Figure 4.2: Social and biophysical methods used for the integrated assessment of ecosystem services use in three villages (Dja area, southeastern Cameroon), including data collection and analysis. Each subsection corresponds to a subtitle of the 'Material and Methods' section. Circled numbers correspond to the four specific objectives of the study. Inputs and outputs of each method are symbolized by lower-case letters from 'a' to 'i'.

3.2.2. Bushmeat use

Based on the daily monitoring of the 55 volunteer households conducted during three months by six trained investigators, we recorded the dietary intake of 3291 meals through structured interviews (five directed questions) and the weighing of bushmeat products (Ngabinzeke *et al.*, 2014; Rastoin and Ghersi, 2010). For each meal, we recorded (i) if the household consumed animal proteins (two levels qualitative variable: yes/no), (ii) the type of proteins (three levels qualitative variable: bushmeat/fish/livestock), and (iii) the number of people eating (qualitative variable). If the meal contained bushmeat, we recorded (iv) if it had been hunted or purchased by the household (two levels qualitative variable). Specifically in Eschiambor village, we weighed undressed meat (quantitative variable) with spring scales (maximum measurement of 10 kg) when possible. We asked (v) the price if bushmeat had been purchased, and for collected bushmeat, we asked respondents to estimate the price of this quantity if they had bought this piece of meat locally (quantitative variable).

For the village of Eschiambor, we computed the mean daily mass of consumed bushmeat in g person^{-1} day^{-1} and the mean daily financial value of consumed bushmeat in FCFA person^{-1} day^{-1} (means of the means of each household), and we extrapolated the mass consumption for a year. Over the whole dataset, and separating each village, we computed the proportion of meals for which bushmeat had been purchased (‘c’ in Figure 4.2).

In order to map the hunting areas for the three villages (Rist *et al.*, 2010), we accompanied volunteer hunters over 651 km with tracking on GPS devices, as well as georeferencing all encountered traps, cartridges, hunting camps, and hunted animals. We generated minimum convex polygons computed on all corresponding GPS points and tracks to map the extent of the hunting zone in the neighborhood of each village (‘d’ in Figure 4.2). We considered a buffer zone of 5 km around each hunting camp as a proxy of the influence of hunters (Hayashi, 2008).

3.2.3. Firewood use

Based on the aforementioned daily monitoring of the 55 volunteer households, we recorded 3367 days of firewood consumption (Fox, 1984). Every evening, we weighed the quantity of firewood that the household estimated to be used until the next evening (quantitative variable), with spring scales (maximum measurement of 50 kg) when possible. Through structured interviews (four directed questions), we recorded (i) if the firewood had been collected by the household or purchased (two levels qualitative variable), with (ii) the corresponding price (quantitative variable). For the analysis of the economic importance of firewood in the overall budget of households, we also recorded (iii) the daily total income (quantitative variable) and (iv) total expenses (quantitative variable) of each household every day. In order to compare the consumption of firewood and timber afterwards, we converted the measures of firewood mass into volume based on the measure of the ‘basic density’ of 21 samples of firewood collected randomly in agricultural areas (average of 0.567 in g cm^{-3}), computed with their oven-dry weight divided by their wet volume (Fearnside, 1997).

Over the whole dataset, we computed the mean daily mass of firewood used in kg $person^{-1}$ day^{-1} (mean of the means of each household) and we converted it into volume, extrapolated for a whole year of consumption, in m^3 $person^{-1}$ $year^{-1}$. We also computed the proportion of firewood mass which has been purchased, the proportion of purchased firewood in the total firewood consumption of buyer households, and the proportion of firewood purchase in their total expenses (‘e’ in Figure 4.2).

In order to map the zones of firewood collection (Kalibo and Medley, 2007), we also accompanied volunteer villagers over 50 km with tracking on GPS devices, as well as georeferencing collection sites. We generated minimum convex polygons computed on all corresponding GPS points and tracks to map the extent of the firewood collection zone in the neighborhood of each village (‘f’ in Figure 4.2). We considered a buffer zone of 100 m around each collection point to consider the extent of agricultural fields where firewood was collected.

3.2.4. Timber use

We randomly sampled 69 households for the quantification of timber use: 12 in Malen I, 24 in Eschiambor, and 33 in Mintoum (corresponding respectively to 75%, 62%, and 42% of the total number of households in each village). We only considered traditional house structure in the estimation of timber use, and either with straw roof or roof plate (Figure 4.3). For each household, we estimated the total volume of timber used, based on the wall surface. We first measured the wood volume used in 293 m^2 of walls corresponding to nine houses, and considering wood poles as cylinders, this allowed computing a mean conversion factor from the wall surface to estimated timber volume used. We additionally measured the volume of boards used in the construction of roofs. Based on structured interviews (two directed questions and one open-ended question), we)asked to the 69 considered households (i) if they had collected or purchased the timber used (two levels qualitative variable). We also asked them to estimate (ii) the durability of their house (quantitative variable, in years), and to mention (iii) the wood species used with local names (open answers).

Over the whole dataset, we computed the mean total volume of timber used to build a house and the proportion of timber volume which has been purchased. Based on the mean estimated durability of houses and the number of permanent residents per household, we converted the total timber volume used in houses into m^3 $person^{-1}$ $year^{-1}$ (‘g’ in Figure 4.2).

Figure 4.3: Traditional house type considered for the estimation of timber use in the integrated assessment of ecosystem services use in three villages (Dja area, southeastern Cameroon). (**A**, **B**) Traditional house structure. (**C**) Making of straw roof. (**D**) Roof plate.

3.2.5. Cultural services use

For the evaluation of cultural services used by local populations (Jaligot *et al.*, 2018), we used structured interviews to question 145 respondents belonging to 83 different households: 15 in Malen I, 24 in Eschiambor, and 44 in Mintoum, corresponding respectively to 94%, 62%, and 56% of the total number of households in each village. We used 14 open-ended questions relative to five different cultural services (R. S. de Groot *et al.*, 2010; Lhoest *et al.*, 2019): cultural heritage and identity, inspiration for culture and art, spiritual experience, recreation, and education (see the detailed list of questions in Appendix 8). We coded answers in ordinal values: '0' value when the respondent totally disapproved, '1' value when the respondent totally approved, and '0.5' value in intermediate situations.

Over the whole dataset, and separating each village, we computed the mean value for all answers relative to a single ES, as a score attributed to the ES (mean of the means of each household; 'h' in Figure 4.2).

In order to map all culturally important sites (Daïnou *et al.*, 2016), we accompanied volunteer villagers to georeference relaxation sites, places of worship, sacred sites and sacred trees. The list of all culturally important sites was previously compiled with villagers during a participatory mapping exercise (Larzillière *et al.*, 2013) conducted in each village ('i' in Figure 4.2).

3.3. Determinants of the use of ecosystem services

We tested five socio-demographic variables acquired at the scale of each household in the population census (‘a’ in Figure 4.2: origin, two levels qualitative variable; ethnic group, two levels qualitative variable; main source of income, four levels qualitative variable; mean daily income, quantitative variable; maximum level of education, four levels qualitative variable) as explanatory variables of the use of the eight ES in 40 univariate linear models (eight linear regressions for the only quantitative explanatory variable (mean daily income), and 32 analyses of variance for the four qualitative explanatory variables). We used as response variables: (i) the mean individual daily consumed mass of bushmeat (kg person^{-1} year^{-1}; ‘c’ in Figure 4.2), (ii) the mean individual yearly consumed volume of firewood (m^3 person^{-1} year^{-1}; ‘e’ in Figure 4.2), (iii) the mean individual yearly consumed volume of timber (m^3 person^{-1} year^{-1}; ‘g’ in Figure 4.2), and (iv, v, vi, vii, viii) the mean scores attributed to the five cultural ES (from 0 to 1; ‘h’ in Figure 4.2). To identify the significant relationships, we computed the *F*-statistics of each linear model and the associated *P*-value (alpha = 0.05).

In order to identify the influence of potential determinants of ES use at the village scale, we mapped the forest cover (in 2000) and the deforestation rates in the neighborhood of each village (over the 2000-2012 period) using geospatial data provided by Hansen *et al.* (2013), as well as the limits of forest allocations, together with the extent of the hunting zones (‘d’ in Figure 4.2), firewood collection zones (‘f’ in Figure 4.2) and culturally important sites (‘i’ in Figure 4.2), all related to the village population size (‘a’ in Figure 4.2).

3.4. Sustainability of the use of provisioning services

In order to assess the sustainability of the use of provisioning services relatively to the extent of their collection zones, we estimated the consumption of bushmeat and firewood for comparison with general estimates of natural production in tropical forests.

For bushmeat, we estimated the total consumption in Eschiambor, extrapolated for a year (average consumption per capita in the village, ‘c’ in Figure 4.2, multiplied by the population size, ‘a’ in Figure 4.2), and divided by the area of the observed zone of bushmeat hunting (‘d’ in Figure 4.2). We then discussed the sustainability of bushmeat consumption, based on the maximum production of wild meat estimated in tropical forests (Robinson and Bennett, 2000). Moreover, we confronted this result to the response of 24 hunters (split among the three villages) who were asked with a single directed question whether bushmeat abundance had evolved since the last decade (two levels qualitative variable: increase or decrease of animal abundance).

For each village, we computed the individual mean consumption of firewood in Mg person^{-1} year^{-1} (‘e’ in Figure 4.2), multiplied by the number of inhabitants (‘a’ in Figure 4.2) and divided by the area of the firewood collection zone (‘f’ in Figure 4.2), itself multiplied by the mean proportion of tree cover (data from Hansen *et al.*, 2013) within a distance of 2 km from the village for considering only the productive forest area where firewood is collected. We then discussed the sustainability of firewood use, based on biomass annual increment estimated in Cameroon agro-forest areas (Djomo *et al.*, 2011).

4. Results

4.1. Quantification of the use of ecosystem services

Among provisioning services (Figure 4.4), local populations consumed a mean of 154 g of bushmeat person^{-1} day^{-1} in Eschiambor (standard deviation = 127 g person^{-1} day^{-1}), corresponding to a daily budget of 88 FCFA person^{-1} (standard deviation = 54 FCFA person^{-1} day^{-1}), and an extrapolation of 56 kg person^{-1} year^{-1}. Animal proteins were consumed in 39% of the 3291 recorded meals (over the three villages), themselves distributed among 58% of bushmeat products (divided between 57% purchased and 43% directly hunted by the households), 37% of fish, and 5% of small livestock (comprising chicken, goat and pork). On average, local populations used 1.8 kg of firewood person^{-1} day^{-1} (standard deviation = 1.3 kg person^{-1} day^{-1}). Only two households out of 55 purchased firewood. This represented 1% of total firewood consumption, but up to 34% of the total firewood consumption of buyer households, although only represented 1.4% of their total expenditures. Each household made use of 3.75 m^3 of timber on average in the construction of its house (standard deviation = 2.17 m^3), in which 21% of timber volume was purchased and 79% was directly extracted from the forest by the household. According to respondents, the mean estimated durability of houses was 35 years (standard deviation = 17 years, average of 21 years for straw roof and 44 years for roof plate). The wood species mainly used and preferred in the construction of houses was sapelli (*Entandrophragma utile* (Dawe & Sprague) Sprague).

Among cultural services (Figure 4.4), the educational importance of the forest was recognized by 86% of respondents, who mentioned the hunting techniques and the NTFP gathering as important knowledge to be transferred to future generations. The forest was perceived by 73% of respondents as an important cultural heritage with vegetal and animal species to be conserved, as well as ancient villages and cemeteries. The forest also provided spiritual experiences to 56% of villagers, comprising sacred trees, sacred sites, places for rites and traditions. While only 27% of respondents declared to ramble in the forests for relaxation purpose without collecting any products, 62% of respondents reported to walk in the forest in order to escape from the problems of the village and 77% enjoyed their time spent in the forest, giving an overall score of 55% for the recreational service. Lastly, the inspiration of forest for culture and art was seen as significant by 25% of respondents, mentioning legends and stories told to children, as well as the inspiration of forests for craftsmanship.

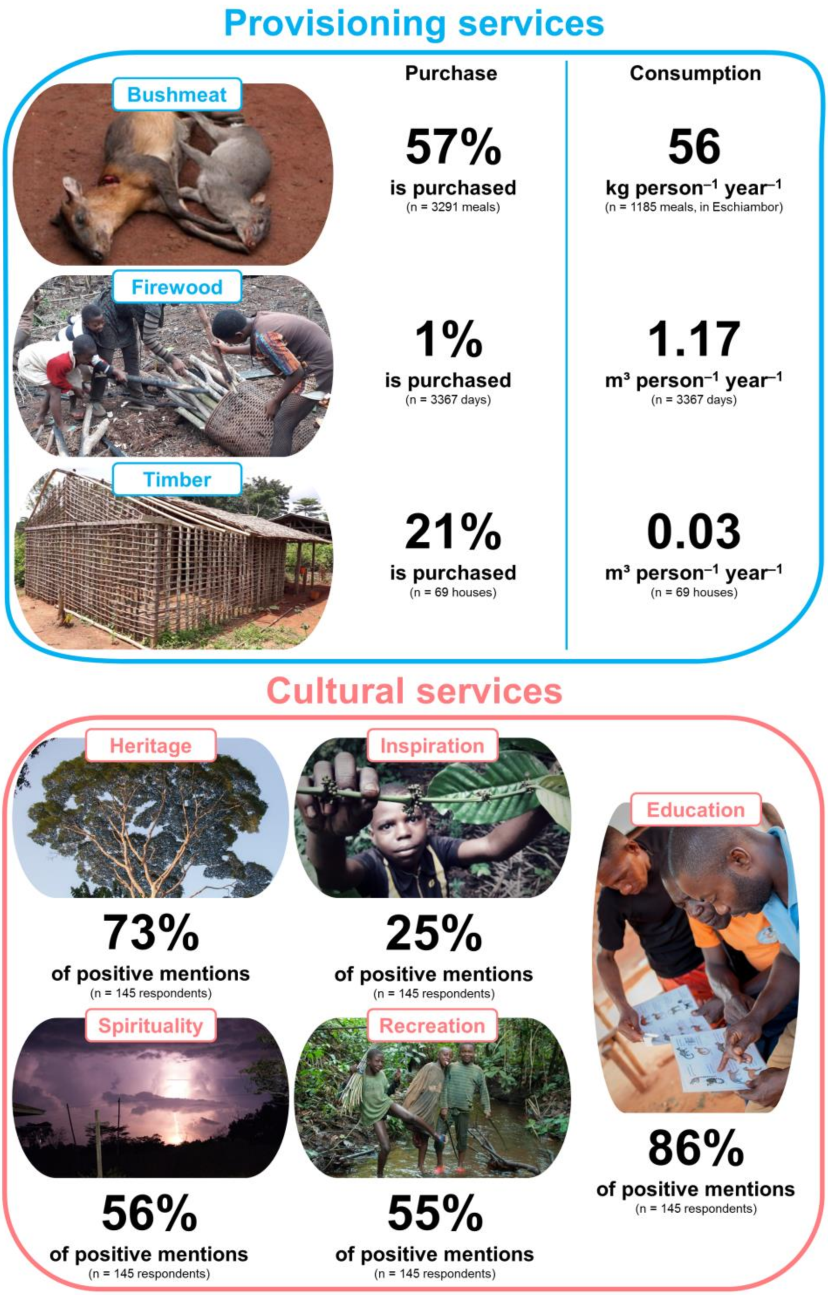


Figure 4.4: Quantification of key provisioning and cultural ecosystem services used by local populations in three villages of the Dja area (southeastern Cameroon). Average values presented here correspond to all households monitored and interviewed. Percentage values of purchase are computed as percentage of meals for bushmeat, and as percentage of the used volume for firewood and timber. The values given for cultural services correspond to the score between 0 and 1 attributed to each ES, which has been multiplied by 100.

4.2. Determinants and mapping of the use of ecosystem services

The three villages had very similar socio-demographic characteristics and household lifestyles, except a high proportion of Baka people in Mintoum (53% of households) and only Bantu people in the two other villages (Appendix 9). In the 40 univariate linear models at the household scale, only the ethnic group was related to two cultural services (Table 4.1): cultural heritage and identity (*P*-value = 0.025), and spiritual experience (*P*-value = 0.044). The Baka people mentioned more frequently than Bantu people the importance of cultural heritage and spiritual experience. All conditions of application of linear models were verified and respected (simple random and independent samples, homoscedasticity, and normal distributions of residuals).

Table 4.1: *P*-values of the 40 univariate linear models between the use of ecosystem services (response variables) and socio-demographic variables at the household scale (explanatory variables) in three villages of the Dja area (southeastern Cameroon). For bushmeat consumption, we only used data acquired in the village of Eschiambor, with only Bantu people.

Ecosystem services	Number of households	Origin	Ethnic group	Main source of income	Mean daily income	Maximum level of education
Bushmeat consumption	13	0.306	-	0.195	0.992	0.551
Firewood consumption	47	0.145	0.125	0.735	0.232	0.054
Timber consumption	32	0.499	0.387	0.334	0.463	0.304
Cultural heritage and identity	43	0.838	**0.025***	0.882	0.795	0.927
Inspiration for culture and art	43	0.236	0.115	0.127	0.645	0.584
Spiritual experience	43	0.424	**0.044***	0.585	0.096	0.448
Recreation	43	0.992	0.558	0.802	0.583	0.076
Education	43	0.873	0.156	0.579	0.434	0.856

We used a total of 1358 georeferenced points of hunting activities (1182 traps, 71 cartridges, 23 hunting camps, and 82 hunted animals), and 117 georeferenced collection sites of firewood for the mapping of the ES use. When considering the use of ES at the village scale, two clear results appeared (Figure 4.5). First, the sparsely populated and isolated village Malen I showed a hunting zone seven times smaller than the two other villages. Meanwhile, people in Malen I consumed less frequently bushmeat (15% of all meals) than in the two other villages (27% of all meals in Eschiambor, and 22% of all meals in Mintoum), and consumed more frequently fish (28% of all meals, against 6% of all meals in Eschiambor and 13% of all meals in Mintoum). Fish in Malen I is caught in the Dja river situated at only two kilometers from the village. Bushmeat in Malen I was also more frequently hunted directly by the consuming households (53% of meals) than purchased, contrary to the two other villages (40% of meals from direct hunting in Eschiambor, and 24% in Mintoum). Second, the isolated village of Malen I showed much lower mentions of the cultural importance of forests for local populations than in the two other villages. In particular, only 33% of respondents in Malen I mentioned the spiritual experience attributed to the forest, compared to 55% in Eschiambor and 72% in Mintoum. Only two cultural sites were mentioned by the inhabitants of Malen I: a sacred tree and an inselberg recognized for its heritage value. In Eschiambor, five culturally important sites were identified: a sacred site, an ancient village where some villagers still maintain ancestral rituals, a cascade considered as a relaxation site, and two sacred trees used for traditional medicine. In Mintoum, the only village where we interviewed Baka people (who constitute 53% of respondents), 19 cultural sites were identified and were mostly linked to the Baka people: four sacred sites, two ancient villages, a tomb, a cascade considered as a relaxation site, and 11 sacred trees either used for traditional medicine or mourning ceremonies.

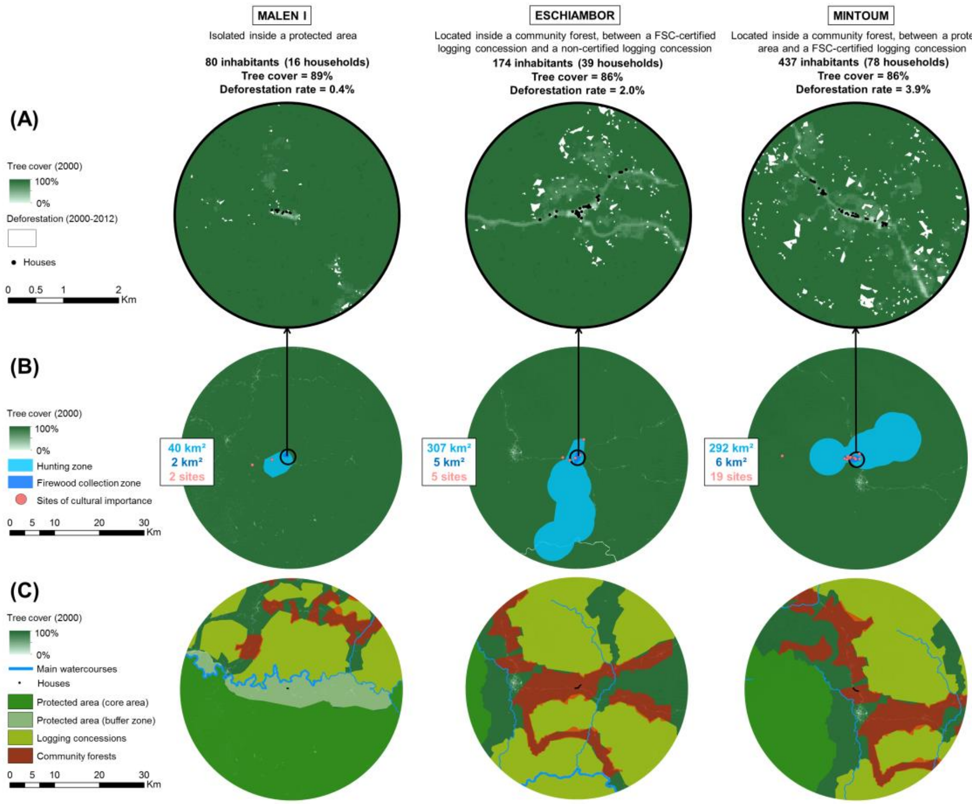


Figure 4.5: Characteristics of the three studied villages in the Dja area (southeastern Cameroon) in which we conducted an integrated assessment of ecosystem services use. (**A**) Tree cover in 2000, tree cover loss between 2000 and 2012 (Hansen *et al.*, 2013), and location of housings in the settlement area of each village. (**B**) Spatial extent of bushmeat hunting and firewood collection zones, generated by minimum convex polygons using all GPS points and tracks recorded during the study. Sites of cultural importance are mapped as points. (**C**) Forest allocations and main watercourses in the surroundings of villages.

4.3. Estimated consumption of provisioning services for discussing sustainability

The total consumption of bushmeat estimated in Eschiambor was 32 kg/km²/year. Moreover, all of the 24 hunters questioned about the evolution of bushmeat abundance noticed a decrease since the last decade. The estimation of total firewood mass used annually in each village was: 0.38 Mg ha^{-1} year^{-1} in Malen I, 0.20 Mg ha^{-1} year^{-1} in Eschiambor, and 0.69 Mg ha^{-1} year^{-1} in Mintoum.

5. Discussion

Here, we conducted the first integrated assessment of ES use by local populations in southeastern Cameroon tropical forests, using both social and biophysical approaches. We identified a high influence of village characteristics (population size, deforestation rate, surrounding forest allocations) on the ES use (Figure 4.5), whereas socio-demographic characteristics of households were much less informative (Table 4.1), as shown for the perceptions of ES supply (Lhoest *et al.*, 2019). Among the three studied villages, the population size, the deforestation rate and the extent of the zones of ES use showed positive correlation (Figure 4.5), and indeed deforestation influences and decreases the ES supply and use (Gillet *et al.*, 2016a).

5.1. Bushmeat consumption

The area of hunting zones around villages varies between 40 km² (Malen I) and 307 km² (Eschiambor). As a comparison, the hunting zones of other villages varied between 170 and 518 km² in the same study area, and between 25 and 600 km² in a larger dataset including villages in Cameroon, Congo, and Central African Republic, the population size being a major determinant of the hunting zone area (Delvingt *et al.*, 2001). In order to compare the extent of forest use among different villages, the use of a spatial occupancy index is suggested (Vermeulen and Karsenty, 2001), defined as the ratio between the area used (here, for bushmeat hunting) and the number of permanent households living in the village. In our study area, the villages show the following indices: Malen 2.5 km²/household, Eschiambor 7.9 km²/household, and Mintoum 3.7 km²/household. These values are all higher than the mean spatial occupancy index of 2.0 km²/household previously reported in this area (Vermeulen and Karsenty, 2001). This may show the relative defaunation around the studied villages, obliging hunters to cover larger areas to get enough animal proteins. The extent of hunting zones largely covers forest allocations where hunting is forbidden (Appendix 1), such as the protected area and logging concessions (also observed previously in the same zone; Delvingt et al., 2001), showing the ineffectiveness of official regulations (Lescuyer, 2013). However, anti-poaching operations can have a dissuasive effect on the preferred directions of hunters (Figure 4.5) in the protected area (preference of Mintoum's hunters for the FSC-certified logging concession) and in the FSC-certified logging concession (preference of Eschiambor's hunters for the non-certified logging concession).

The high frequencies of bushmeat consumption reported (34% to 76% of meals with proteins, corresponding to 15% to 27% of all meals) confirmed the high dependence of rural populations on forest ecosystems to meet their dietary needs (Nasi *et al.*, 2011; Robinson and Bennett, 2000). These results are comparable with another dietary monitoring conducted in the same area, showing that 12% of 21% of all meals contained bushmeat (Auzel, 2001). In Malen I, the majority of consumed bushmeat was directly hunted by the consuming households (53%), whereas most bushmeat was purchased in Mintoum (74%), which is situated in the most deforested part of our study area. The unit price of bushmeat increases with deforestation

(Gillet *et al.*, 2016c), inducing a negative feedback loop towards even more hunting, and further in the forest, due to the context of high poverty.

We found that the inhabitants of Eschiambor consumed a mean of 154 g of bushmeat person^{-1} day^{-1}, which is comparable to other measures in the Dja area, going from 75 to 164 g person^{-1} day^{-1} (Delvingt *et al.*, 2001; Dethier, 1998). It is 3.6 times more than the daily dietary recommendations of 43 g of meat from the EAT-Lancet report (Willett *et al.*, 2019). It is 3.8 times higher than the average consumption of bushmeat from forest sources in Cameroon which is reportedly 41 g person^{-1} day^{-1} considering FAO statistics for the country (Speedy, 2003), knowing that not all populations are directly depending on forest resources. It is under the average meat consumption in industrialized countries which is 241 g person^{-1} day^{-1} (Reynolds *et al.*, 2014).

Bushmeat consumption reported to the area of the hunting zone in Eschiambor (32 kg/km²/year) was lower than the measures of 93 to 173 kg/km²/year reported in villages of the same zone in 2001 (Delvingt *et al.*, 2001). It is also below the sustainability standard of the maximum production of wild meat roughly estimated between 150 and 200 kg/km²/year in tropical forests (Robinson and Bennett, 2000). Even if bushmeat consumption in Eschiambor could seem to be sustainable, inventories of mammal populations have shown that only small animals remain in these areas close to villages and roads due to past hunting pressure (Lhoest *et al.*, 2020). Indeed, a high and growing hunting pressure induces a decline in the biomass of forest vertebrates, with large-bodied preferred game species declining rapidly (Koerner *et al.*, 2017; Poulsen *et al.*, 2011). Moreover, the human density of one person per km² suggested as the maximum density in order to maintain sustainable bushmeat consumption (Robinson and Bennett, 2000) is eight times less than the population density in our study area. The lack of accurate biological data for each hunted species (such as the age at first reproduction, fecundity, and maximum longevity) does not allow us to precisely quantify the sustainability of bushmeat hunting in the study area (Fa and Brown, 2009). However, it has already been suggested that the hunting practices are not sustainable in Cameroon (Fa *et al.*, 2003) and in the Dja region in particular (Vermeulen *et al.*, 2009). In a sustainable bushmeat exploitation scenario, bushmeat could only contribute to 10–18% of the whole protein supply across Cameroon and other sources of protein would be needed from the agricultural sector (Fa *et al.*, 2003). Many forest areas in Central Africa are already considered as almost empty of wildlife (Wilkie *et al.*, 2019), and 55% of species are being hunted unsustainably in Central Africa according to the IUCN Red List (Taylor *et al.*, 2015).

5.2. Firewood and timber consumption

Whereas most studies on firewood consumption were conducted in urban areas (Eba'a Atyi *et al.*, 2016), the use of firewood in this rural and forested area was 1.8 kg person^{-1} day^{-1}. This is 20% higher than the average consumption throughout

Africa (1.5 kg person^{-1} day^{-1}; Pesche *et al.*, 2016), and comparable to the average consumption in Cameroon (1.9 kg person^{-1} year^{-1}, according to FAO – ForeStat). This is three times the daily consumption of 0.6 kg person^{-1} day^{-1} measured in the dry forest area in the Far North Region of Cameroon where firewood is overexploited (Charpin and Richter, 2012). The consumption of charcoal remains negligible in Cameroon rural areas (Eba'a Atyi *et al.*, 2016).

There are few studies about the use of firewood in forested rural areas in Central Africa and Cameroon, but there are even less studies about the use of timber for the construction of houses. Our results showed an average use of 3.75 m³ of timber per household in the construction of its house (without considering possible repairs), and general rough estimates across Africa give an average of 0.5 to 6 m³ per household (Pesche *et al.*, 2016). When converting the total volume to the volume used per person and per year (based on the estimated durability of houses), we obtained a consumption of 0.03 m³ person^{-1} year^{-1}, whereas data from the Far North Province in Cameroon showed a volume of 0.01 m³ person^{-1} year^{-1} in urban areas and 0.05 m³ person^{-1} year^{-1} in rural areas (MINFOF, 2017). With more income being allocated to housing improvements, local populations mentioned that they would seek to use mud bricks and roof plate.

Whereas local populations did not show any preferences about wood species for firewood collection, some species were preferred over others for house construction, in a desire for better resistance to humidity and xylophagous insects. Sapelli was the most used wood species in timber construction: the FSC-certified logging concession logged 0.07 m³ ha^{-1} year^{-1} of sapelli in 2013, whereas the living stock of that species was about 3.81 m³ ha^{-1} in the study area (Cellule Aménagement Pallisco and Nature+, 2015). In comparison, based on the maximum area of a community forest (5000 ha) and the population size of the most populated village in our study area (Mintoum, 437 inhabitants), the total volume of timber used for house construction could reach 0.003 m³ ha^{-1} year^{-1} for all species combined, which is 23 times less than the volume logged in the logging concession only for the sapelli species. In volume, the consumption of firewood was 39 times higher than the consumption of timber for the construction of houses in our study area. We then considered that the timber extraction for local use in the construction of houses has only a limited impact on forest ecosystems but that the sustainability of firewood collection can be questioned. We estimated the total firewood mass used annually in each village (0.38 Mg ha^{-1} year^{-1} in Malen I, 0.20 Mg ha^{-1} year^{-1} in Eschiambor, and 0.69 Mg ha^{-1} year^{-1} in Mintoum). Based on a biomass annual increment of 5.46 Mg ha^{-1} year^{-1} estimated in Cameroon agro-forest areas (Djomo *et al.*, 2011), the consumption of local populations would constitute approximately up to 13% of the natural growth of the wood resource (7% in Malen I, 4% in Eschiambor, and 13% in Mintoum). This only constitutes a rough estimate of the sustainability of firewood use but it gives an informative order of magnitude. Of course, firewood is not the only wood resource extracted from these forests but it shows than firewood collection is not a major threat on forest ecosystems in this area. Moreover, firewood is a by-product of shifting agriculture and is only collected as dead wood in agricultural areas (Gazull and Gautier, 2015). Directly linked to the total population size, it is the extent of agricultural zones that impacts the forest cover and potentially leads to net deforestation (de Wachter, 1997).

5.3. Cutural services use

Among the important cultural services that we identified here, cultural heritage, spiritual experience and inspiration were also frequently perceived as abundant in the same area (Lhoest *et al.*, 2019). The educational value of forest ecosystems for children in the acquisition of local knowledge has also been highlighted in this zone (Gallois *et al.*, 2015). The differences in cultural services identified among the three villages could be explained as follows. First, the rare mentions and use of cultural services in Malen I are probably due to the fact that this village only exists since the foundation of the protected area in 1950. Local populations may have developed only few cultural connections with forest ecosystems. The populations of the two other villages migrated from nearby locations in the current logging concessions during the recent decades, and local people consider ancient villages as places of worship (Vermeulen, 2000). Second, the higher proportion of Baka people in Mintoum may explain the high cultural importance of forests for local populations in this village. Baka people systematically evaluated cultural services as more important than Bantu people did, and they identified many sites of cultural importance (Figure 4.5). The only Baka respondents were interviewed in Mintoum (53% of households interviewed about cultural services in this village). Despite a recent trend of sedentarization and involvement in agricultural activities instead of their ancestral hunter-gatherer nomadic lifestyle (Oishi, 2016), Baka people still maintain many rituals and traditions linked to the forest (Joiris, 1998; Leclerc, 2012). The different cultural preferences among villages may also be related with the different ethnolinguistic groups of Bantu people: mainly Badjoué in Malen I, and mainly Nzimé in Eschiambor and Mintoum (Porro *et al.*, 2001).

Altogether, our results underline what may be referred as to the *culturality* of ES (Pröpper and Haupts, 2014). Despite their importance for ES assessment (Scholte *et al.*, 2015), cultural services have been far less studied than provisioning services. This is likely due to the lack of adequate assessment framework and the complexity to address them with traditional quantitative approaches (Chan *et al.*, 2012; Díaz *et al.*, 2018; Milcu *et al.*, 2013). Going further than the classic western concept of cultural services (such as recreation), the recent works on the concept of Nature's Contributions to People (developed in the frame of the Intergovernmental Platform on Biodiversity and Ecosystem Services – IPBES) starts from acknowledging the importance of non-instrumental values and the related interplay between emotional, social and cultural factor (Pascual *et al.*, 2017). It raises the important roles of culture, indigenous and local knowledge in understanding the links between people and nature (Díaz *et al.*, 2018). This concept suggests working both at a general level and at a context-specific level, the latter giving room for multiple ways of understanding and categorizing relationships between people and nature in the reach of sustainability.

6. Conclusions

Our study quantified and mapped the use of important ES provided by tropical forests to local populations in southeastern Cameroon. We confirmed that population size, deforestation rate, and forest allocations may be of particular importance in depicting the use of forest ES, whereas socio-demographic characteristics of households have a limited influence. Forest-related cultural services were partly shaped by ethnicity, with Baka people attributing much more cultural importance to forest ecosystems than Bantu people. Among provisioning services, we identified the sustainable use of firewood and timber by local populations, but we showed that past high hunting pressure limited the availability of bushmeat. Methods and results of ES assessment as ours must be implemented in concrete management strategies at local and regional scales in order to achieve sustainability, by engaging local communities into the assessment process for the social inclusiveness (Brown and Weber, 2011; Jaligot *et al.*, 2018) and the political legitimacy of assessment findings (Brondizio and Tourneau, 2016).

5

General conclusion

1. Major findings

The aim of this thesis was to assess the conservation value of tropical forests, as well as the supply of ES, and their use by local populations, in three contrasted forest allocations (a protected area, a FSC-certified logging concession, and three community forests) located in the Dja area, in southeastern Cameroon.

The conservation value of tropical forest areas was found to be mainly determined by the proximity to human settlements (*i.e.*, villages and roads) and activities (*i.e.*, management or forest allocation) rather than by local habitat characteristics (**Chapter 2**). As expected, the three studied forest allocations showed contrasted conservation values. The protected area has a high conservation value and is essential in landscape conservation strategies. In a large forest landscape matrix, production forests can play a buffering role for extending the conservation estate in the periphery of protected areas, if managed adequately. Indeed, the largest threatened mammal species (in terms of body mass) and the largest dung beetle species (in terms of body length) were detected in the protected area and the most remote areas of the logging concession, better preserved from human influence. Community forests were found to be much more defaunated and degraded. Even if the two inventoried taxonomic groups (mammals and dung beetles) responded differently to human-induced disturbance, species richness was the highest in the protected area and the lowest in the community forests. The high species replacement (*i.e.*, spatial turnover) among forest allocations suggests integrating conservation initiatives in many sites, and not only in single large protected areas.

Besides the quantification of forest conservation value, we conducted interviews in order to assess the perceptions of the ES supplied by forests to rural populations in the Dja area (**Chapter 3**). The ES perceived as the most important for local populations were found to be provisioning and cultural services. By comparing the frequencies of perceptions of ‘important’ and ‘abundant’ ES as rough proxies of their absolute significance and abundance, all important ES were perceived to be supplied abundantly by forest ecosystems, except bushmeat. Forest allocation was the main determinant of the perceptions of ES supply, considering the different user rights for rural people’s access among forest allocations.

The ES for which the supply was perceived as the most variable in **Chapter 3** (namely provisioning and cultural services) have been quantified with complementary biophysical and social methods in **Chapter 4**, through a detailed assessment, monitoring, and mapping of ES use. The use of ES was linked to forest allocations, village population size and deforestation rate. As also shown for the perceptions of ES supply, no strong link between ES use and socio-demographic characteristics of respondents has been made, except the influence of ethnicity on the cultural heritage value and spirituality. We found that the forest area really used by local populations for hunting can reach 30 700 ha, and thus largely exceeds the maximum area of community forests which is 5000 ha (Lescuyer, 2013; Vermeulen, 2000). We confirmed that bushmeat is the ES which is used in the least sustainable way by local populations, pointing the major challenge of reconciling wildlife conservation and sustainable hunting in this social-ecological system, where bushmeat is crucial as a valuable proteic and caloric intake in the diet of rural people, besides carbohydrates and other agricultural products.

2. Forest land allocations: conclusions and research perspectives

As expected, the measured indicators of biodiversity and ES differed among forest allocations (Table 5.1). Biodiversity was clearly higher in the protected area than in the two forest allocations, where the remaining species mostly depends on the distance to human settlements. This implies to gather all forest management entities for communicating on the implementation of concrete conservation strategies based on a coordinated mapping and preservation of the ecological network and corridors.

Provisioning services (bushmeat, firewood and timber) were mostly supplied in the community forests and in some areas situated inside the logging concession, whereas the access to the protected area for collecting forest products is forbidden and villagers are relatively discouraged by the anti-poaching operations. This shows the effectiveness of law enforcement for conservation outcomes, and the potential to implement new models of forest resources governance for the participatory management of overlapping rights of logging companies and rural populations (Karsenty and Vermeulen, 2016).

Regulating services are hypothesized to be dependent on forest cover, structure and composition (Brandon, 2014), which were all relatively similar among the studied forest allocations, with, however, less forest biomass and carbon stocks in the community forests (Fonteyn, 2017). Regulating services were then not measured in the thesis, but most of them (for instance water quality regulation, climate regulation, or protection against natural hazards) were assumed to be supplied at almost comparable levels among the studied forest allocations, all being characterized by the same forest cover of 90% (Appendix 1). The protection of forest cover and the struggle against deforestation and forest degradation will be particularly important in the coming years in Central Africa (and in Cameroon in particular), with the increasing pressures of shifting agriculture, firewood collection, timber logging, mining, and hunting (Abernethy *et al.*, 2016; Gillet *et al.*, 2016b).

Cultural services were much more context specific than other ES and were less related to particular forest allocations. For instance, the number of culturally important sites in a village was mainly related to the history of the village and to the ethnic origin of the population. But nonetheless, the cultural services in the protected area were systematically at a lower level than in the community forests and the logging concession, except for tourism. This calls for the explicit consideration of the local cultural context for the integration of rural populations in forest management strategies, such as in the FSC certification (Daïnou *et al.*, 2016). This also shows that the low cultural significance of the protected area to local populations complicates their appropriation of conservation policy.

Table 5.1: Synthesis of the indicators of biodiversity and ecosystem services measured in each forest allocation, with three levels from '+' to '+++' indicating increasing values of biodiversity/ecosystem services.

Indicators	Protected area	Logging concession	Community forests
Biodiversity	+++	++	+
Provisioning services	+	++	+++
Regulating services	+++	+++	++
Cultural services	+	+++	+++

Beyond forest biodiversity and ES, the studied forest allocations have other contributions to local livelihoods that should not be neglected. Besides conservation, protected areas have a potential for tourism, awaireness raising, educational activities, and scientific research. Logging concessions contribute to the economic and rural development, and offer job opportunities to local populations. Beyond their spatially limited impacts on forest ecosystems, community forests may contribute to local livelihoods and quality of life, by generating employment and income for local development projects, despite highly variable outcome throughout the country (Vermeulen, 2014). Opportunities exist for the improvement of community forestry in Cameroon, including an enhancement of partnerships and collaboration between community forests and external actors such as local NGOs and the private sector (Minang *et al.*, 2019).

This thesis did not aim to assess the effectiveness of land use regulations, contrary to Bruggeman *et al.* (2015) who focused on the effects of forest allocations on deforestation and forest degradation in southeastern Cameroon. In this thesis, we rather measured proxies of biodiversity and ES in order to identify their main determinants, comprising forest allocations among other explanatory variables. Our results focused on single examples of forest allocations in a unique social-ecological system, and do not allow drawing general conclusions about forest allocations in Cameroon or Central Africa. However, our results inform about the potential of the three forest allocations for biodiversity conservation and ES supply, based on a specific and concrete assessment.

Studied indicators of biodiversity and ES did not allow assessing the existence of a potential leakage effect between different forest allocations, *i.e.*, a 'displacement of land uses to near or remote sites' (Meyfroidt *et al.*, 2020), as an influence of human activities (such as agriculture) between contiguous forest allocations at their edge or in the buffer zone between them. Indeed, no biodiversity or ES indicator was mapped throughout the whole forest allocations, but forest allocations were used as baseline stratification for the punctual sampling of all indicators. Moreover, for biodiversity indicators, no sampling sites were set up at less than 500 meters from the edges of studied forest allocations in order to avoid any edge effects on diversity measures. For the identification of potential leakage effect in a study of biodiversity or ES mapping, it would be recommended to statistically compare measured indicators in different buffers at edges between areas of interest (Bruggeman *et al.*, 2015).

The results obtained for each forest allocation are useful for improving forest management, but the interpretation of results must go further than the sole status of forest allocations. It is worth noticing that the studied 'forest allocations' encompass the legacy of the accumulated land use history of forest areas on the long term, and not only the current land allocation. Forest management has evolved differently in the different studied areas, at different time scales, and even before the set up of current land allocations. However, most measured indicators of biodiversity and ES are relatively dynamic and mostly depend on recent forest ecosystem dynamics, even if the three studied forest allocations may not constitute an exactly similar initial baseline.

In particular, for the quantification of the conservation value of forest areas (**Chapter 2**), the limited dataset and number of sites hinders a definite disentangling of the independent effects of logging impacts and the proximity to villages. For instance, in the logging concession, the areas logged 20-30 years before inventory appeared as more depauperate in mammal species than the areas logged more recently (10-20 years before inventory). The shape of the rarefaction curve for mammal species in the zone logged 20-30 years before inventory was also very different than the shape of all other rarefaction curves, showing stronger variations of slope than the other curves and intersecting them (Figure 2.2). Besides the higher proximity to villages of the zone logged 20-30 years before inventory than the zone logged 10-20 years before inventory, the logging concession engaged in FSC certification in 2008, which led to reduced-impact logging practices with potentially measurable consequences on inventoried taxonomic groups. Moreover, mammal and dung beetle populations may react rapidly to the evolution of human pressures and associated forest dynamics (Nichols *et al.*, 2007).

Two methodological perspectives may be considered in future research in order to definitely disentangle the effects of past logging, hunting pressure and initial forest conditions on inventoried biodiversity. First, pseudoreplication is inherent in this kind of study sampling only one forest allocation of each kind. For drawing some general conclusions, one could use a nested sampling design: for example, ten clusters could be defined, located in several regions or countries, in order to represent the diversity of social-ecological systems in the study area (*e.g.*, Central Africa). Each cluster would consist of a group of four sites, each site corresponding to different land allocations: protected area, logging concession, community forest, and monoculture plantation such as oil palm. The four sites studied within each cluster would be close to each other and would be selected in order to control for spatially explicit confounding factors: initial GIS analyses would be used to select study sites where forest composition, distances to villages, roads, and major rivers, population density, and management history are comparable, based on all existing data.

Second, measures of local impacts of human disturbances (logging, hunting, and agriculture) and of natural conditions (vegetal and animal species, climate, and soil) should be used to better inform the history of study sites. Classical forest biodiversity monitoring of plant or animal species could be supplemented by more spatially extensive surveys recording multiple types of data about the forest status, changes and uses (Salk *et al.*, 2020), comprising direct observations and interview-based data, such as the extensive mapping of logging damages (stumps, logging roads, skid trails, and logyards), the identification of tree species composition, the measure of forest structure parameters, or the participatory mapping of hunting zones.

3. Reconciling conservation and sustainable use of tropical forests?

Contrary to major international policy orientations towards the quantification and valuation of regulating services (for instance carbon storage in REDD+ scheme, regulating services in FSC certification, or payments for environmental services), our results showed that the major challenge identified in the Dja social-ecological system is the reconciliation of wildlife conservation, food security, and sustainable hunting practices.

The overharvesting of bushmeat in the study area is due to two main reasons. First, sustainable hunting is not possible with a population density of 8 people/km² if local populations depend on bushmeat as their principal source of proteins (Robinson and Bennett, 2000), driving an overharvesting over time. Second, the evolution of village-based subsistence hunting towards generalized commercial use for generating some income reinforces even more the overharvesting, sometimes going until food insecurity for some households in order to access other services such as medicines, energy, or education (van Vliet *et al.*, 2010). Indeed, based on the monitoring of hunting catches in the three studied villages (**Chapter 4**), only 40% of bushmeat was eaten by hunters' households, and 60% was sold. Moreover, 19% out of a group of 32 hunters interviewed about their hunting practices declared that they generally sell all of their hunting offtake. The rate of bushmeat sale increased up to 77% of hunting catches in Mintoum, which is the village with the easiest access to a supply chain in the city of Lomié, located at only 8 km. Bushmeat consumption was also the lowest in this village, most probably due to the search for income by hunters' households by selling hunting products.

At the village scale, it could be possible to assess the willingness of local populations to use alternative sources of proteins and to lower their bushmeat consumption in order to design concrete wildlife management strategies and improve sustainability. It could be performed by conducting a price elasticity analysis including the fate of each hunting catch (self-consumption or sale with the corresponding price), compared to the price of other available proteins in the village. The data collected for the thesis did not allow such analysis. Indeed, for ethical reasons and in accordance with the volunteer hunters, we did not record such data in order to guarantee confidentiality of hunting activities and work confidently with local populations. Wilkie *et al.* (2005) have conducted such economic analyses in Gabon with 1208 households. They did not find a significant influence of the prices of substitutes for bushmeat on the bushmeat consumption, but variations in the price and consumption of bushmeat influenced the consumption of fish. These authors recommend that policy makers should use economic levers such as taxation, or better law enforcement to lower the demand for bushmeat.

The most efficient way to develop forest management strategies in order to improve sustainability is to use a prior social approach with all relevant stakeholders, as performed in **Chapter 3** for the quantification of the perceptions of ES supply. Such methods can produce strong evidence for social levers underpinning behavioral changes among forest users.

According to local populations during our interviews, the high pressure on wildlife mainly results from generalized unemployment in this region. Despite frequent conflicts between hunters and ecoguards in the protected area, during the interviews local populations often considered themselves as the best potential protectors of nature, if only they could depend on something else than bushmeat for generating income (*i.e.*, important relational value, Chan *et al.*, 2016; see the section '6. Integration of ecosystem services in tropical forest management'). In particular, they frequently mentioned the 'ECOFAC' project (funded by the European Union in early 2000's) as the panacea to struggle effectively against illegal hunting and poaching, and this project was frequently perceived as an example to be followed. The ECOFAC project created new income for local communities, comprising people involved in awaireness-raising, controls, traditional medicine management, or the implementation of alternative proteins production systems. Unfortunately, the permanence of such major projects, funded by international donors during a limited time period of a few years, often shows a failure on the long term if the financial self-sufficiency is not reached by local stakeholders. The same applies to the long term funding of nature conservation that is an issue per se. The participation of local populations in participatory repressive enforcement programs (Vermeulen *et al.*, 2009) and awaireness-raising campaigns, if coordinated on the long-term by external actors (*i.e.*, the private sector or NGOs) is probably the best way to limit dramatic impacts on endangered species.

During interviews, local communities also mentioned fishing as an alternative source of income and proteins for the future. Despite highly variable yields between seasons, such as for NTFP gathering (which are also highly variable from a year to another), fishing is not forbidden in logging concessions. The major determinant of a potential fish supply chain would be the proximity to large rivers (Abe'ele Mbanzo'o, 2001). Local populations also recognize a spatial structuration of fishing rights with particular techniques among different rivers, which must be considered to avoid any conflicts in fishing management. Abe'ele Mbanzo'o (2001) tracked an organized supply chain of fish products from a village near the Dja river to points of sale up to 530 km, in Douala. The incomes generated by fishing households were comparable to those obtained from hunting activities (25 455 FCFA/year per active fisher, in 1998). According to interviewed local populations, fish stocks remain sufficient in the study area for local consumption, and only artisanal fishing techniques are used. Of course, such as for wildlife populations, it would be essential to monitor the evolution of fish populations to avoid surexploitation if this activity were to intensify.

As a concrete initiative to reconcile wildlife conservation, food security and local livelihoods, the project *Sustainable Wildlife Management* is currently implementing an approach for the local development of a sustainable and legalized supply chain of bushmeat for some species, based on the understanding of wildlife populations' dynamics (through camera trapping), as well as the monitoring of hunting practices (through georeferencing of all hunting signs and catches) and bushmeat consumption in pilot villages in Gabon, and in the nearby town of Lastourville (~12,000 inhabitants). The rural population density is much lower around Lastourville (1 person/km²) than in our study area in southeastern Cameroon (8 people/km²). Consequently, practical recommendations and conclusions of this project may only be applicable in contexts of low population density, and probably not in more densely populated areas such as the Dja area.

Population density is a crucial parameter to be considered in the design of any development or management project. Studying the individual contributions of rural households to deforestation in the surroundings of Kisangani (Democratic Republic of Congo), Moonen *et al.* (2016) showed that population density and associated market access are the main determinants of deforestation. This rural area has a population density of 9.8 people/km², with an average of 1209 inhabitants/village, which is five times higher than the average of 230 inhabitants/village in our studied villages in southeastern Cameroon. This suggests an important supply chain of all forest products towards the nearby large city of Kisangani (~1 million inhabitants), whereas the main city in our study area is Lomié, with only ~19,000 inhabitants. This led to strong differences among individual households in their contributions to environmental changes, notably deforestation, and forest use in these Congolese villages, contrary to our study where only few socio-demographic determinants of ES use were identified among households.

4. Mammals and dung beetles as indicators of biodiversity

Mammal and dung beetle species were inventoried with the assumption that they are representative of the overall biodiversity and conservation value of studied forest areas. These groups are sensitive to different environmental disturbances and both contribute to major ecological processes (Nichols *et al.*, 2009). The determinants of mammal and dung beetle populations have already been discussed in **Chapter 2**, in the section '5.2. Differential response of mammals and dung beetles'.

Ground-dwelling mammals are frequently considered as a unique indicator group of biodiversity (De Iongh and Persoon, 2010). In the specific context of southeastern Cameroon and considering the importance of hunting to local populations, mammals constitute an important taxonomic group to be assessed for their major contribution to hunting catches and their significant roles in ecological mechanisms. In particular, large mammals have been decimated over the last few decades and are at a higher risk of extinction than smaller animals due to a combination of environmental factors and intrinsic traits (Cardillo *et al.*, 2005). The extinction of hunted species following overhunting results in the alteration of major ecological functions: disruption of trophic webs, limitation of seed dispersal, tree recruitment and forest regeneration, without mentioning other cascading effects (Abernethy *et al.*, 2013; Poulsen *et al.*, 2018; Redford, 1992; Terborgh *et al.*, 2008). Whereas our results and meta-analyses reported a relatively weak impact of selective logging on mammal populations (Gibson et al., 2011; Putz et al., 2012), the detrimental effects of hunting on mammal populations are clear and undoubted. The accessibility to hunters and poachers, directly linked to the proximity to villages and roads, is the main driver of mammal populations and defaunation (Benítez-López *et al.*, 2017; Clark *et al.*, 2009; Koerner *et al.*, 2017; Laurance *et al.*, 2006).

Dung beetles are frequently used as bioindicators as their sampling is more cost-effective than almost any other taxonomic group in tropical forests (Cajaiba *et al.*, 2017; Gardner *et al.*, 2008; Klein, 1989). Moreover, they contribute to various ecological processes: nutrient fertilization and cycling, plant growth, or seed dispersal, among others (Nervo *et al.*, 2017; Nichols *et al.*, 2008). The logging intensity has been identified as a major determinant of dung beetle richness and biomass (Burivalova *et al.*, 2014; França *et al.*, 2018), alongside the extent of bare ground cover (Bicknell *et al.*, 2014), fragmentation, and habitat modification (Nichols *et al.*, 2007).

Dung beetles species richness is reported to be correlated to the number of mammal species due to their ecological relationship: dung beetles use faeces of mammals as food and nesting resources (Bogoni *et al.*, 2016) and they can detect volatile compounds at great distances (Frank *et al.*, 2018). Most of them exhibit habitat preferences and dung beetle assemblages are associated to land use (Frank *et al.*, 2017). Whatever the latitudinal region, mammal communities generally shape dung beetle assemblages and overhunted areas would present less diverse dung beetle communities (Nichols *et al.*, 2009). Mammals and dung beetles were not sampled at exactly the same locations in this thesis and therefore it was not possible to assess any relationship between the two groups. Little is known on forest dung beetle communities in Central Africa (Cambefort and Walter, 1991; Frank *et al.*, 2018), but the cascading effects of overhunting on mammals and associatied dung beetle community structure and function have been described in other tropical regions (Figure 5.1; Nichols *et al.*, 2009).

Other taxonomic groups than mammals and dung beetles might be of interest as indicators of biodiversity and forest conservation value in response to human disturbance (Lindenmayer and Burgman, 2005; Lindenmayer *et al.*, 2000). Of course, inventorying all groups of organisms composing biodiversity is highly time-consuming. For instance, it took up to 1000–6000 hours for inventorying nematodes, termites, and canopy beetles on a gradient from nearly primary, through old-growth secondary and plantation forests, to complete cleared plots in the Mbalmayo Forest Reserve in south-central Cameroon (Lawton *et al.*, 1998). Moreover, such inventories require strong taxonomical expertise for a variety of groups.

In order to assess the effects of human disturbance on biodiversity, an essential step is to identify the diverse forms of disturbance, with potential diverse effects on different taxa (Sodhi *et al.*, 2009). In particular, logging may affect different elements of forest ecosystems, through canopy loss (impacting taxa such as butterflies and litter ants) and soil compaction (impacting soil-dependent taxa such as termites). Whereas tree replantation may mitigate tree cover loss, soil compaction can be a permanent effect of logging (Barlow *et al.*, 2007; Stork *et al.*, 2017). For any group selected as a biodiversity indicator, it is required to have a basic understanding of the changes in species composition induced by forest disturbance, rather than just measuring species richness that can conceal species replacement (Bengtsson *et al.*, 2000; Gardner *et al.*, 2009; Lindenmayer and Franklin, 2002). In Cameroonian tropical forests, Stork *et al.* (2017) recommend the inventory of butterflies and litter ants as useful indicator groups, with the compromise of their high sensitivity to multiple drivers of disturbance and the reasonable time needed for their inventory and identification.

Finally, the best way to evaluate the impacts of human disturbance on biodiversity will always be a long-term monitoring of selected taxa. It guarantees to measure the dynamics of species and functional composition following disturbance, without any confusion with potential spatial species turnover among studied sites, namely beta-diversity (Lindenmayer and Laurance, 2012; Ramage *et al.*, 2013).

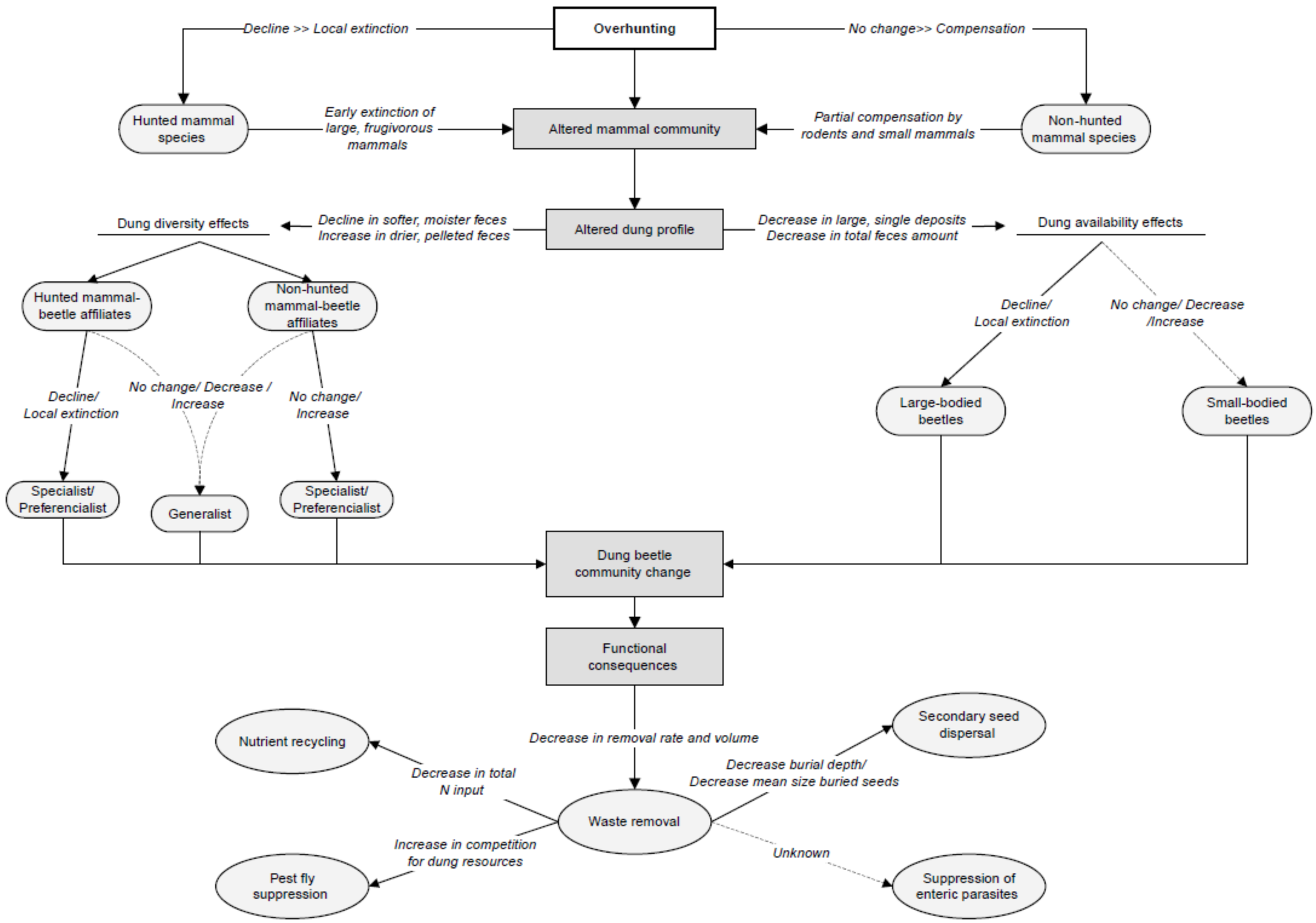


Figure 5.1: Conceptual model of the impacts of overhunting on dung beetle community structure and function in tropical forests (extracted from Nichols et al., 2009).

5. Interactions between biodiversity and ecosystem services

The relationships between biodiversity and ES are poorly understood in all ecosystems (Mace *et al.*, 2012), and it is even more true for tropical forests. There is no evidence that a high biodiversity systematically provides many ES. For instance, the relationship between tree species richness and carbon storage in tropical forests has recently regained interest, because conserving at the same time biodiversity and carbon would be an adequate perspective for both conservation and climate issues. Based on expert opinion, Alamgir *et al.* (2018) found a spatial congruence between biodiversity and the climate regulation service in northeastern Australian tropical forests. However, a recent compilation of forest biological inventory data shows no clear relationship between tree diversity and carbon storage, either at the pantropical scale or within continents (Sullivan *et al.*, 2017). This indicates that conservation and management strategies focusing solely on diversity or carbon will inevitably not consider all important forest areas. Both biodiversity and ES thus need to be explitly considered when designing conservation and management policies.

Based on the conceptual framework adopted in this thesis (Figure 1.4), biodiversity, as a conceptual component of forest ecosystems, is hypothesized to be related to the supply of ES. It was beyond the scope of the thesis to test for causal relationships between biodiversity and ES, whereas the objective was to assess biodiversity and ES individually, as well as identifying their main determinants. For practical and logistical reasons, all biodiversity and ES indicators were not measured in the same exact locations and during the same exact periods. In particular, each biodiversity and ES indicator had to be sampled and measured at a specific spatial scale. For instance, mammals are not inventoried in the same way as dung beetles, or trees (Fonteyn, 2017). The inventory of mammal diversity (biodiversity) followed international standard protocols (TEAM Network, 2011), with camera traps distributed over the three forest allocations and focused on a limited zone of influence (2 km² around each camera trap), whereas the monitoring of hunting (ES use) was centered on villages and hunters moving towards forest areas, along tens of kilometers. Each biodiversity and ES indicator was directly related to individual determinants such as spatial and social variables, but it was not possible to analyze the interactions among all indicators because of the different spatial and temporal scales.

Even if it is particularly challenging, it would be possible to test the potential effect of biodiversity on the supply of ES using a two-step approach, through: (i) the definition of a theoretical causal model, (ii) the setting of an adequate sampling design and the use of adequate temporal and/or spatial techniques for the statistical analysis of data.

First, a theoretical causal model should be defined, articulating the mechanisms assumed to link biodiversity and ES supply. A key challenge is to better understand the process of co-production of ES by social-ecological systems, by linking together indicators of biodiversity, ecosystem functions, and ES (Bennett *et al.*, 2015). This would require to identify the potential roles of the different components of biodiversity at various scales, from genes to landscapes (Balvanera *et al.*, 2017; Díaz *et al.*, 2006), in the supply of ES. In particular, it is needed to analyze the sensitivity of ES to the variability of biodiversity, the associated resilience of ES to environmental change such as deforestation (Gillet, 2016) or forest degradation (Dupuis *et al.*, 2020), as well as all corresponding ecological processes (Mace *et al.*, 2012). Resilience is defined as the rate of return to an equilibrium state, the ability to withstand change, or combinations of these (Ghazoul and Chazdon, 2017). For example in Southeast Asia, massive deforestation and conversion to oil palm monocultures has lead to a loss of resilience, notably to fires. Concretely, several studies focused on the relationships between biodiversity and the unique category of regulating services (*e.g.*, Egoh *et al.*, 2009, in South Africa, or Labrière *et al.*, 2015, in Borneo). Harrison *et al.* (2014) undertook a systematic literature review analyzing the linkages between 16 biodiversity attributes and 11 ES, showing that most relationships were positive between paired indicators (Table 5.2). Their results give some insights for the definition of potential biodiversity-ES relationships (Figure 5.2) to be studied in any specific social-ecological system.

Table 5.2: Synthesis of positive (↑) and negative (↓) relationships identified between biodiversity attributes and ES in a systematic literature review across 530 studies (Harrison *et al.*, 2014).

	Species abundance	Species richness	Species diversity	Species size/ weight	Mortality rate	Functional richness	Behavioural traits (pollination)	Behavioural traits (biocontrol)	Community/ habitat area	Community/ habitat structure	Primary production	Aboveground biomass	Belowground biomass	Stem density	Community/ habitat/ stand age	Litter/ crop residue quality
Provisioning services:																
Timber production	↑	↑↓														
Freshwater fishing	↑	↑		↑	↓						↑					
Freshwater provision									↑↓					↓	↓	
Regulating services:																
Water purification		↑							↑							
Water flow regulation									↑	↑					↑	
Mass flow regulation		↑							↑	↑		↑	↑			
Atmospheric regulation		↑	↑	↑	↓					↑		↑	↑		↑	↑
Pest regulation	↑	↑				↑		↑	↑	↑						↑
Pollination	↑↓	↑					↑									
Cultural services:																
Recreation (species)	↑↓	↑	↑	↑												
Landscape aesthetics									↑	↑						

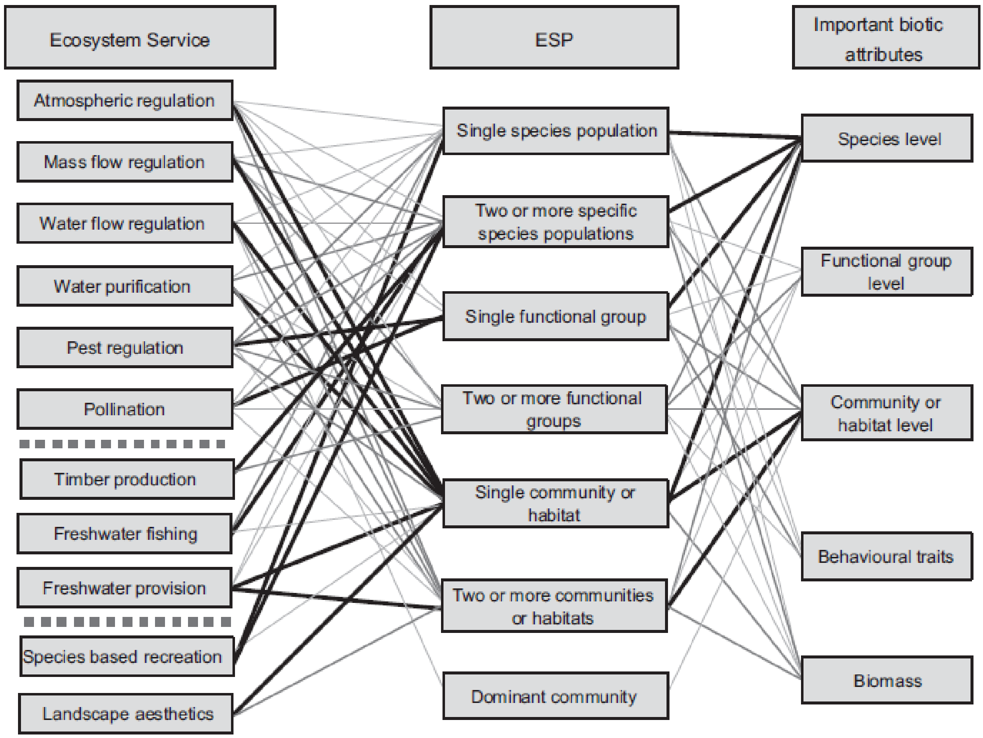


Figure 5.2: Relationships among groups of biodiversity attributes ('Important biotic attributes'), Ecosystem Services Providers ('ESP'), and ES ('Ecosystem Service'), for 11 ES included in a systematic literature review of 530 studies (Harrison *et al.*, 2014). The thickness of lines is correlated to the number of studies showing some evidence for the considered linkage.

Secondly, a quasi-experimental design (*i.e.*, sampling design) should be developed in order to effectively test the theoretical causal model between biodiversity attributes and ES. All variables of interest (biodiversity attributes and ES indicators) could be measured in a number of sites distributed along a gradient of deforestation or forest degradation (from sites with very low to very high deforestation or degradation levels, such as oil palm monoculture plantations). Several gradients could be sampled in distinct regions or countries, in order to represent the diversity of social-ecological systems throughout the study area (for instance across Central Africa). Depending on the budget of the study for data collection, spatial and/or temporal statistical analyses could be conducted. On the one hand, a temporal monitoring of all variables of interest should be encouraged, in order to avoid the influence of different intrinsic characteristics of studied social-ecological systems (*e.g.*, tree species composition, soil characteristics, or ethnic groups among local populations). Temporal approaches allow the use of rigorous impact evaluation techniques (Before-After-Control-Impact design) and identifying causality relationships among measured indicators (*e.g.*, Le Velly and Dutilly, 2016, developed such methodological insights applied to schemes of payments for environmental services), based on panel data (*i.e.*, multi-dimensional data acquired through measurements over time). On the other hand, the definition of a large number of sites is necessary in order to gain sufficient spatial representation of social-ecological conditions across a large study area of inference[2]. All measured variables of biodiversity and ES could be compared within and between gradients based on matching techniques (*i.e.*, evaluation of the effect of a treatment on outcome variables in treated units in comparison to control units), enabling analyses at both local and regional scales (*e.g.*, Miteva *et al.*, 2015; Wendland *et al.*, 2015).

6. Integration of ecosystem services in tropical forest management

The integrated assessment of ES (combining social, ecological, and economic approaches) offers many important perspectives for tropical forest management. Integrated ES assessment constitutes a holistic way to consider all stakeholders and challenges in a specific social-ecological system, from the conservation of biodiversity to the use of ES by several beneficiaries. The multidimensional nature of ES calls for integrated valuation approaches (Martín-López *et al.*, 2014). In the specific context of environmental conflicts, the inclusion of diverse ES values in assessments allows to pursue social and environmental justice (Jacobs *et al.*, 2016). There are many different purposes to conduct an ES assessment, further than only for academic and scientific research, going from decision making to awareness raising or to resolution of conflicts (Figure 5.3). It is also critical to adapt the choice of ES assessment methods based on available time and means. Numerous ES assessment tools exist and their use has to be aligned with specific needs and context. As an example, Hugé *et al.* (2020) provide guidance to ES practitioners for the selection of ES assessment tools in the African context.

[2] A serial alternating panel approach could be implemented in order to cycle the measures in a series of panels, improving both temporal and spatial representativity of the sampling sites.

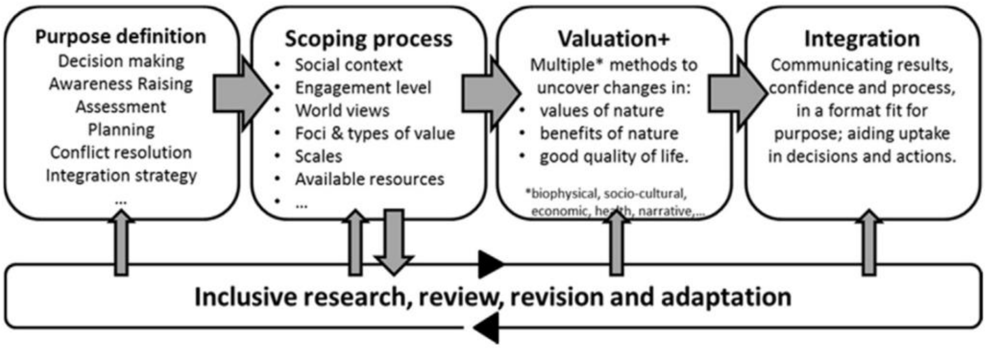


Figure 5.3: State-of-the-art of integrated valuation and its main components (extracted from Jacobs *et al.* 2016).

As an important recommendation for future research, an ES study should initially identify the beneficiaries of ES before any data collection. The identification of all ES beneficiaries in studied social-ecological systems is crucial for any relevant ES assessment (Quijas *et al.*, 2019), even if it is generally neglected by researchers, especially in (tropical) forest ecosystems (Cruz-Garcia *et al.*, 2017). Complementarily, the analysis of the use and management of ecosystems by these ES beneficiaries is essential (R.S. de Groot *et al.*, 2010; Haines-Young and Potschin, 2010). During this thesis, some indicators have been measured but were not used in data analysis and valorization: physicochemical parameters of water quality (pH, conductivity, concentration of dissolved oxygen, concentration of nitrates, concentration of ammonium) in 92 rivers, tree species composition and vegetal aboveground biomass in 44 1-ha plots, and logging damages (stumps, logging roads, skid trails, and logyards) in and around the 44 vegetation plots. All of these data were collected without an appropriate identification of ES beneficiaries, in particular for regulating services (water quality regulation, or climatic regulation through carbon storage).

The social and participatory approaches used in ES assessment emphasize the high importance of integrating all local stakeholders for creating social inclusiveness (Brown and Weber, 2011; Jaligot *et al.*, 2018) and reinforcing the political legitimacy of findings (Brondizio and Tourneau, 2016). The use of social methods at the local scale has been recognized as crucial in ES assessments (Díaz *et al.*, 2018). For instance, using role-playing games is suggested as an original way to make rural communities aware of the consequences of unsustainable forest use and management (Fauvelle and Garcia, 2018; Ponta *et al.*, 2019; Waeber *et al.*, 2019) and ES social approaches are formative for all participating stakeholders (Kenter *et al.*, 2011). Participatory approaches considering the interests and needs of diverse stakeholders also allow to identify sources of conflicts and to implement concrete solutions to avoid them in the future (Arias-Arévalo *et al.*, 2017). For instance in Central Africa, many conflicts arise among forest stakeholders: rural populations often express negative attitudes towards the state and logging companies. Considering all stakeholder viewpoints allows identifying the reasons for conflicts and proposing solutions, such as the securement of user rights to forest land and resources for local communities (Samndong and Vatn, 2012).

The needs of forest-dependent populations are rarely prioritized in forest management (Bele *et al.*, 2015; Persha *et al.*, 2011; Robinson, 2016), and the engagement of rural populations in forest management has been limited in southeastern Cameroon (Carson *et al.*, 2018a; Donn *et al.*, 2016; Fa *et al.*, 2003; Gbetnkom, 2008; Sanchez, 2000). However, both Bantu and Baka people in the Dja area express the desire to be included in sustainable solutions for forest management (Carson *et al.*, 2018b), proposing concrete perspectives: (i) to foster employment and income-generating activities for replacing poaching; (ii) to develop protein alternatives to bushmeat, through poultry, pig or fish farming; and (iii) to promote the autonomy of rural communities for the long-term appropriation of livelihood-based initiatives. Including local populations in conservation and management strategies is indispensable for implementing long-term sustainability (Figure 5.4).

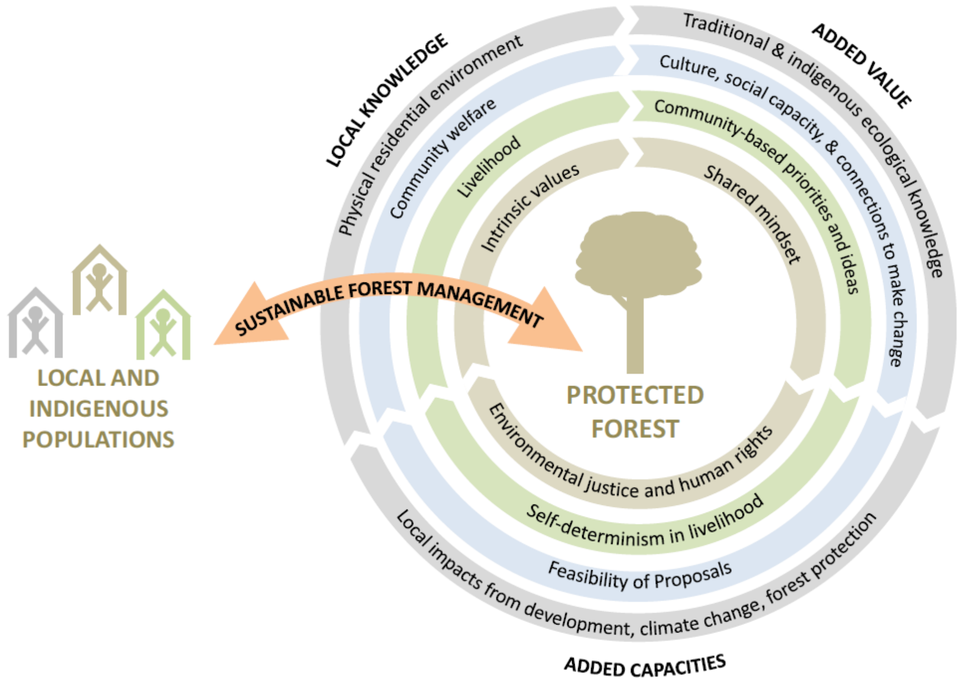


Figure 5.4: Benefits of local populations' knowledge for the development of sustainable forest conservation and management strategies (extracted from Carson *et al.* 2018).

All the interviews conducted during the thesis provided multiple informations about relational values (Chan *et al.*, 2016), even if they were not assessed explicitly. Relational values are defined as ‘the importance attributed to meaningful relations and responsibilities between humans and between humans and nature’ (Arias-Arévalo *et al.*, 2017). When talking about improving sustainability through behavioural changes, relational values constitute a key concept going further than environmental and social approaches that are traditionally not connected together (Chan *et al.*, 2018). For instance, in response to the questionnaire used in **Chapter 3** about the perceptions of ES supply, local populations very frequently expressed their relations with their social-ecological system, in the following ways:

- ‘We are nothing without the forest!’
- ‘In the village, if you don't have the forest, you don't even live!’
- ‘We live from the forest: our culture is a forest culture, with our Bakas brothers.’
- ‘Everything is useful in the forest!’
- ‘The forest is the basis of human life here, before agriculture.’
- ‘We were born in the forest.’
- ‘The Bakas and Bantu have pacts with the forest and close relations with it.’
- ‘Those who do not have the forest are in pain.’
- ‘Traditional pharmacopoeia is our strength!’
- ‘The forest protects a lot!’
- ‘We learn at school not to waste the forest!’
- ‘The forest ecosystem is violated with logging!’

Such qualitative results (and much more of them which are not described in this thesis) constitute valuable insights for the better understanding of the populations’ perceptions of ecosystems and the implementation of behavioural change incentives for a sustainable use of forest ecosystems (Chan *et al.*, 2018).

Alongside the use of social approaches which give rapid information without the absolute need of long periods of field work, ecological monitoring of ES and biodiversity give complementary information for sustainable management and conservation. For instance, the effectiveness of a substantial conservation intervention can be tested through a before/after monitoring of large mammal populations. Similarly, the consequences of the supply of alternative proteins in a local market could be measured by the monitoring of the evolution of the hunting offtake and supply network, as indicators of behaviour changes. The usefulness of ecological approaches has also been developed in the previous section for the evaluation of biodiversity-ES relationships.

Economic values of ES are also useful in order to add another value domain in integrated assessments, in particular for identifying the hidden costs that are not captured by other methods. However, whereas most ES studies only focused on economic values (Satz *et al.*, 2013), economic valuations of ES should never be considered alone in the decision making process.

The ES concept offers new perspectives for tropical forest management applications. The FSC is currently developing new criteria of forest certification based on the assessment of ES, and particularly regulating services. Indeed, the resilience of the provision of ES to local populations is considered as a priority for the stability and adaptability of social-ecological systems in the climate change context. However, there is a great risk that including ES in FSC certification would further complicate the approach and make it more and more expensive and elitist in Central Africa, in the already fragile remaining FSC-certified logging companies. Schemes of payments for environmental services (PES) also depend on reliable and standardized measures of ES to be implemented efficiently and fairly, notably through economic valuation.

Several concrete initiatives in protected areas and community forest concessions also try to include ES in their management plans through participatory approaches, such as in the '*Programme de maintien de la biodiversité et gestion durable des forêts*' implemented in the Democratic Republic of Congo by the GIZ. In the frame of the EVAMAB[3] project ('Economic valuation of ecosystem services in Man and Biosphere Reserves'), Hugé *et al.* (2020) classified ES assessment tools adapted to the context of African Biosphere Reserves, based on input and output data, skills required, ES addressed, time constraints and purpose of the assessment. This classification of ES assessment tools answers concrete management issues based on what is important, measurable, and urgent to address in any specific protected area.

Furthermore, instead of targeting a single allocation to forest land, the uses that are not mutually exclusive could be overlaid so that to maximize the benefits from a single place to all stakeholders. For instance, a new conceptual model of 'Concession 2.0' has been suggested in Central Africa, built through an inclusive multi-stakeholder governance platform for the management of overlapping rights (Karsenty and Vermeulen, 2016). This allows the potential valorization of several forest ES (such as timber, NTFP or tourism) benefiting to all forest stakeholders. As already mentioned, a focus on conflict anticipation and management is critical in Central African forests, in particular between rural populations and logging companies (Samndong and Vatn, 2012). This could be initiated through an initial participative evaluation of ES and a concurrent SWOT (Strengths, Weaknesses, Opportunities, and Threats) analysis of the local social-ecological system. Such project would also benefit from an analysis of the effect of the provisioning of revenues to local populations on the sustainability of forest use. As an example of how a Concession 2.0 might work, SFM Africa and The Grande Mayumba Development Company (GMDC) have implemented an investment iniative[4] in

[3] http://www.biodiv.be/evamab

[4] http://www.sfmafrica.com/projects/gabon

southern Gabon where forestry, ecotourism, agribusiness, fisheries, and conservation are managed together. Such a model needs careful negotiations and locking of the rights of local populations, including local employment, training, and revenue sharing for social equity and legitimacy.

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Appendices

Appendix 1: Characteristics of each forest land allocation and subzones. Area was estimated using existing polygons (World Resources Institute, 2012) or manually digitized polygons based on planning documents for the buffer zone of the protected area. Mean forest cover in 2000 and deforestation rate between 2000 and 2012 were estimated using data from Hansen *et al.* (2013).

	Land allocation types						
	Protected area		**Logging concession**				**Community forests**
	Core area	Buffer zone	Production	Conservation	Protection	Agroforestry	
Area (hectares)	526,155	207,584	287,533	45,594	6,789	856	13,466
Mean forest cover (%)	89.6	89.5	90.7	90.2	89.9	90.9	89.7
Deforestation rate (%)	0.0	0.2	0.1	0.1	0.1	1.5	1.5
Hunting	Prohibited	Regulated*	Regulated*	Regulated*	Prohibited	Regulated*	Regulated*
NTFP	Prohibited	Allowed	Allowed	Allowed	Prohibited	Allowed	Allowed
Deadwood	Prohibited	Allowed	Allowed	Allowed	Prohibited	Allowed	Allowed
Living wood	Prohibited	Allowed	Prohibited	Prohibited	Prohibited	Allowed	Allowed
Agriculture	Prohibited	Allowed**	Prohibited	Prohibited	Prohibited	Allowed**	Allowed

*Authorized for self-consumption only, with traditional selective techniques, only for non-protected species

**Current agricultural occupation zone, but prohibition to extend agricultural areas beyond

Appendix 2: Quantification of habitat variables ‘forest degradation’ and ‘canopy openness’ (Chapter 2).

In order to quantify forest degradation in the surroundings of mammal and dung beetle sampling sites, we performed a supervised classification with the maximum likelihood method based on satellite imagery. We used the blue, green, red, and near infrared bands of two Sentinel-2 images, mosaicked in a sole one, acquired on the 25 January 2016, with a 10 meters pixel size. Reference data (9640 reference points) were defined from a combined visual interpretation of the Sentinel-2 image and Google Earth data for better spatial resolution. Four classes were identified: (i) dense forest matrix (comprising dense forest stands and swamp forests), (ii) degraded forests (comprising forest visually impacted by both logging and shifting agriculture) and crops, (iii) bare soil (roads and villages) and (iv) water surface (rivers). We later used a majority filter with a sliding square window of 3 x 3 pixels to smooth the resulting raster. The classification performance was assessed based on the Kappa statistic derived from the confusion matrix. We defined buffer zones around biodiversity sampling points to compute a metric of forest degradation based on the classification raster. Around each camera trap, we considered a 700 meters buffer zone to potentially influence the detection of mammals, considering the recommended distance of 1.4 kilometers between two cameras for mammal inventories in tropical regions (international protocol of TEAM Network, 2011). Around each dung beetle trap, we considered a 75 meters buffer zone, considering that the traps could influence these insects up to 50-100 meters (Larsen and Forsyth, 2005). We computed the proportion of pixels classified as degraded forest in those circular windows around each biodiversity sampling site.

To estimate canopy openness above dung beetle pitfall traps, we took five hemispherical photographs per trap, at 1.5 meters of height and at sunrise: one photo directly above the trap and four photos at 10 meters from the trap in the direction of the four cardinal points. Vegetation below 3 meters of height was cleared beforehand. The percentage of canopy openness is the percentage of open sky seen from beneath a forest canopy and was calculated with GLA software (Frazer *et al.*, 1999). The percentage of canopy openness associated to each trap was the mean of the five values obtained for each trap.

Appendix 3: Pearson's correlation matrices of extrapolated species richness, and environmental variables, for mammals (A) and dung beetles (B) (**Chapter 2**).

A 

Environmental variables	Mammal species richness (Y) extracted from individual-based rarefaction curves for different numbers of detection events (X)									
	Y for X = 10	Y for X = 20	Y for X = 30	Y for X = 40	Y for X = 50	Y for X = 60	Y for X = 70	Y for X = 80	Y for X = 90	Y for X = 100
Distance to the nearest road	-0.04	0.29	0.25	0.25	0.34	0.28	0.27	0.40	0.48	0.33
Distance to the nearest river	0.49	0.31	0.22	0.22	0.33	0.14	0.20	0.12	0.16	0.16
Distance to the nearest village	0.40	0.50	0.32	0.32	0.43	0.27	0.42	0.41	0.49	0.33
Forest degradation	0.05	-0.16	-0.30	-0.30	-0.26	-0.31	-0.20	-0.35	-0.36	-0.30
Protected area	0.06	0.35	0.38	0.38	0.37	0.39	0.33	0.49	0.49	0.42
Logging concession	0.30	0.05	-0.12	-0.12	-0.02	-0.16	0.03	-0.15	-0.09	-0.13
Community forests	-0.40	-0.46	-0.32	-0.32	-0.41	-0.29	-0.42	-0.41	-0.49	-0.35

B 

Environmental variables	Dung beetle species richness (Y) extracted from individual-based rarefaction curves for different numbers of individuals (X)									
	Y for X = 10	Y for X = 20	Y for X = 30	Y for X = 40	Y for X = 50	Y for X = 60	Y for X = 70	Y for X = 80	Y for X = 90	Y for X = 100
Distance to the nearest road	0.68	0.65	0.67	0.57	0.59	0.58	0.57	0.57	0.53	0.55
Distance to the nearest river	-0.24	-0.17	-0.25	-0.25	-0.22	-0.20	-0.23	-0.20	-0.14	-0.20
Distance to the nearest village	0.44	0.48	0.61	0.59	0.58	0.60	0.58	0.60	0.52	0.56
Canopy openness	-0.47	-0.40	-0.50	-0.47	-0.52	-0.54	-0.57	-0.53	-0.52	-0.53
Forest degradation	-0.29	-0.36	-0.37	-0.34	-0.33	-0.27	-0.24	-0.28	-0.25	-0.29
Protected area	0.60	0.57	0.60	0.51	0.51	0.52	0.51	0.51	0.48	0.49
Logging concession	0.09	0.20	0.29	0.38	0.39	0.39	0.42	0.44	0.41	0.43
Community forests	-0.67	-0.71	-0.82	-0.79	-0.81	-0.82	-0.82	-0.84	-0.79	-0.81

Appendix 4: List of mammal species inventoried (Chapter 2).

Species	Mean number of independent detection events per camera working during 87 days				IUCN status
	Protected area	Logged 20-30 years before	Logged 10-20 years before	Community forests	
Atherurus africanus	12.6	13.4	5.8	5.7	Least Concern
*Atilax paludinosus**	3.4	1.2	0.3	0.2	Least Concern
Bdeogale nigripes	1.7	0.4	0.2		Least Concern
Cephalophus callipygus	8.2	2.0	1.9	0.3	Least Concern
Cephalophus castaneus	3.2	2.4	1.3	0.3	**Near Threatened**
Cephalophus nigrifrons	0.1				Least Concern
Cephalophus silvicultor	7.0	1.4	0.4	0.3	**Near Threatened**
Cephalophus sp.	0.3		0.3	0.2	/
Cercocebus agilis	0.2	2.6	1.1	0.8	Least Concern
Civettictis civetta				0.2	Least Concern
Cricetomys emini	30.0	21.2	34.3	48.0	Least Concern
Crossarchus platycephalus	1.6	0.8	0.8	0.5	Least Concern
Dendrohyrax dorsalis			0.1	0.2	Least Concern
Funisciurus isabella	22.9	30.8	9.6	24.5	Least Concern
Funisciurus pyrropus	1.2	7.6	0.6	0.7	Least Concern
Genetta servalina	3.6	2.4	0.3	0.8	Least Concern
Manis gigantea	0.6				**Vulnerable**
Manis spp.	0.3	1.0	1.1	0.5	**Vulnerable**
Nandinia binotata	0.4	0.2	0.7	1.2	Least Concern
Neotragus batesi	0.1		0.6		Least Concern
Pan troglodytes	0.3		0.3		**Endangered**
Philantomba congica	49.4	7.2	9.7	2.8	Least Concern
Potamochoerus porcus	1.6		0.3		Least Concern
Protoxerus stangeri	4.2	16.8	3.3	7.3	Least Concern
Rodentia spp.	5.0	10.2	9.1	20.2	/
Tragelaphus gratus	0.7				Least Concern

*The detection events recorded for *Atilax paludinosus* (Marsh Mongoose) also include the detection events of *Xenogale naso* (Long-nosed Mongoose), but we were not able to distinguish the two species on acquired images.

Appendix 5: List of dung beetle species inventoried and references for the identification (**Chapter 2**).

Species	Number of individuals collected (24 pitfall traps in each forest allocation)		
	Protected area	**Logging concession**	**Community forests**
Alloscelus combesi			1
Amietina larochei		13	
Caccobius elephantinus	1		
Catharsius gorilla	78	33	65
Catharsius gorilloides	1	2	5
Catharsius lycaon	44	52	12
Chalconotus cupreus	1		
Copris phungae subsp. *Gabonicus*	16	2	3
Diastellopalpus conradti	4	15	11
Diastellopalpus laevibasis	8		1
Diastellopalpus murrayi	3	4	3
Diastellopalpus noctis	10	7	15
Diastellopalpus sulciger	29	18	23
Garreta cf *diffinis*	1		
Heliocopris coronatus	6	3	3
Heliocopris helleri	2	3	1
Heliocopris mutabilis	2	6	3
Lophodonitis carinatus	4	1	
Milichus inaequalis			1
Milichus merzi	6		
Mimonthophagus apicehirtus	2		
Neosaproecius trituberculatus	1		1
Neosisyphus angulicollis	10	17	30
Onthophagus atronitidus	162	1	2
Onthophagus barriorum			2
Onthophagus biplagiatus		3	
Onthophagus cf picturatus		1	
Onthophagus densipilis	78	27	204
Onthophagus denudatus	2	6	
Onthophagus depilis	2	2	
Onthophagus dorsuosus	1		
Onthophagus erectinasus	1	9	1
Onthophagus fuscidorsis	633	562	577
Onthophagus graniceps	2		
Onthophagus intricatus	79	22	3
Onthophagus justei	42	9	18
Onthophagus laminosus	1		6
Onthophagus macroliberianus	2		
Onthophagus montreuili	6	3	29
Onthophagus orthocerus	65	51	1
Onthophagus pilipodex	1	1	
Onthophagus pseudoliberianus	3	2	2
Onthophagus rufipodex	1		3
Onthophagus strictestriatus	6	1	
Onthophagus sulcatulus	11	15	1
Onthophagus umbratus	36	14	13

Onthophagus vesanus	2		
Onthophagus sp. 1		6	
Onthophagus sp. 2	1	4	1
Onthophagus sp. 3		2	
Onthophagus sp. 4	1	2	
Onthophagus sp. 5	6	2	
Onthophagus sp. 6	3	1	
Onthophagus sp. 7		6	
Onthophagus sp. 8	1	2	
Onthophagus sp. 9		2	
Onthophagus sp. 10		2	1
Onthophagus sp. 11	11		1
Onthophagus sp. 12	2		
Onthophagus sp. 13	2		3
Onthophagus sp. 14	1		
Pedaria ovata	24	16	7
Pedaria spinithorax	7		
Proagoderus semiiris	142	131	282
Pseudopedaria grossa	33	6	8
Pseudosaproecius validicornis		1	8
Sisyphus arboreus	76	42	1
Sisyphus bayanga	4	8	
Sisyphus sp.	4	1	
Sisyphus walteri	182	109	9
Tomogonus crassus			1

Dung beetle species were identified using the following references:

Branco, T., 1990. Essai de révision des genres du "groupe" stiptopodius : le genre *Neosaproecius* nov. (Coleoptera : Scarabaeidae). *Annales de la Société Entomologique de France (N.S.),* 26(4) : 595-599.

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Josso, J-F & Prevost, P., 2000. Révision du genre *Diastellopalpus. Magellanes, Collection Systématique*, 3 : 1-138.

Josso, J-F & Prevost, P., 2015. Révision du genre *Pedaria* Laporte, 1832. *Magellanes, Collection Systématique*, 26 : 1-160.

Montreuil, O., 2015. Le genre *Neosisyphus* Müller en Afrique (Coleoptera, Scarabaeidae, Sisyphini). *Catharsius, La Revue*, 12(1) :1-36.

Montreuil, O., 2016. Nouveaux *Sisyphus* Latreille, 1807, du groupe *seminulum* : le complexe *arboreus* (Coleoptera, Scarabaeidae, sisyphini). Bulletin de la Société entomologique de France, 121(2) : 167-174.

Moretto, P., 2010. Les Scarabéides coprophages de Bayanga en République Centrafricaine (Coleoptera, Scarabaeidae). *Bulletin de la Société entomologique de France,* 115(4) : 455-477.

Moretto, P., 2017. *Heliocopris eryx* (Fabricius, 1801) et ses formes. Description d'une espèce et de 2 sous-espèces nouvelles. (Coleoptera, Scarabaeidae, Coprini). *Catharsius, La Revue,* 14 : 23-40.

Moretto, P. & Genier, F., 2010. Nouvelles mentions d'espèces de Scarabéides coprophages pour le Parc National du Niokolo-Koba (Sénégal) et descriptions de quatre nouveaux *Onthophagus* (Coleoptera, Scarabaeidae). *Catharsius, La Revue*, 01 : 1-17.

Orbigny, H. d'., 1913 [1913-1914]. Synopsis des Onthophagides d'Afrique. *Annales de la Société entomologique de France,* 82 : 1-742.

Appendix 6: Main characteristics of the 225 respondents for the assessment of ES perceptions (numbers of respondents for each level of socio-demographic variables and age ranges of respondents; **Chapter 3**). In the main occupations: *Salaried* comprise the staff of the logging concession, other workers, the Conservation Service of the protected area and teachers; *Mixed* comprise respondents who acknowledged having more than one occupation; *Officials* correspond to all representatives of the State, Forestry Administration, and community forests committees; *Others* comprise merchants, tourist guides and taxi men.

		Land allocation type			
		Protected area (n = 75)	**Logging concession** (n = 75)	**Community forests** (n = 75)	**All respondents** (n = 225)
Gender (n)		16 ♀ 59 ♂	16 ♀ 59 ♂	18 ♀ 57 ♂	**50 ♀ 175 ♂**
Age: mean [minimum - maximum]		46 [20 - 79]	38 [18 - 62]	45 [15 - 75]	**43 [15 - 79]**
Ethnicity (n)	Badjoué	62	13	22	**97**
	Nzimé	0	2	39	**41**
	Ndjem	0	3	3	**6**
	Baka	2	9	4	**15**
	Other Cameroonian	11	38	7	**56**
	Foreigner	0	10	0	**10**
Main occupation (n)	Farmer	33	20	31	**84**
	Salaried	15	45	5	**65**
	Mixed	17	4	22	**43**
	Student	3	5	5	**13**
	Official	1	1	8	**10**
	Other	4	0	2	**6**
	Fisherman	2	0	0	**2**
	Hunter	0	0	2	**2**

	Main occupation							
Ethnicity	Farmer	Salaried	Mixed	Student	Official	Other	Fisherman	Hunter
Badjoué	43	16	22	6	4	4	2	0
Nzimé	15	3	17	0	4	1	0	1
Ndjem	1	3	1	1	0	0	0	0
Baka	12	2	0	0	0	0	0	1
Other Cameroonian	13	35	3	2	2	1	0	0
Foreigner	0	6	0	4	0	0	0	0

Appendix 7: *P*-values of explanatory variables of ES perceptions obtained from the 16 logistic regressions (**Chapter 3**), modelling the probability of positive answers for each individual ES (in lines) as a function of the six explanatory variables (in columns). *P*-values were adjusted with the Benjamini and Hochberg (1995) method to account for multiple comparisons, controlling the false discovery rate.

Services	Land allocation	Deforestation	Gender	Age	Ethnicity	Occupation
Vegetal NTFP	1.000	0.273	0.574	0.852	0.627	0.968
Meat (hunting)	0.430	0.679	0.247	0.679	0.291	0.026
Fish (fishing)	0.132	0.079	0.754	0.210	0.210	0.574
Firewood	<0.001	<0.001	0.273	0.974	0.079	0.138
Timber	0.007	<0.001	0.026	0.901	0.009	0.079
Traditional medicine	0.574	0.962	0.627	0.614	0.261	0.901
Cultural heritage and identity	1.000	0.614	0.079	0.901	0.249	0.336
Tourism	<0.001	0.590	0.091	0.901	0.574	0.562
Inspiration for culture	<0.001	0.114	0.514	0.044	0.053	0.212
Spiritual experience	0.009	0.185	0.562	0.974	0.073	0.671
Recreation	0.574	0.614	0.562	0.901	0.132	0.574
Water quality regulation	0.574	0.341	0.519	0.704	0.009	0.562
Climate regulation	0.247	0.079	0.433	0.212	0.671	0.679
Air quality regulation	0.614	0.277	0.574	0.331	0.247	0.923
Natural hazard mitigation	0.974	0.679	0.247	1.000	0.679	0.701
Soil formation and regeneration	0.901	0.901	0.210	0.614	0.430	0.901

Appendix 8: List of 14 open-ended questions asked to 145 respondents for the evaluation of five cultural services (**Chapter 4**).

Cultural services	Open-ended questions
Cultural heritage and identity	Does the forest have heritage, cultural, or symbolic value for you?
	Are there animal or vegetal species to conserve for the future?
	Do you know any cemeteries or ancient villages in the forest?
Inspiration for culture and art	Are there legends and stories about the forest?
	Are the craftsmen inspired by the forest?
Spiritual experience	Do you practice any forest-related rituals or traditions?
	Are there sacred trees in the forest?
	Are there sacred sites in the forest?
	Have sacred sites retained the same importance than before?
Recreation	Is it pleasant to go into the forest?
	Do you ramble in the forest to relax without collecting anything?
	Do you sometimes go into the forest to escape the problems of the village?
Education	Is it the forest important for children's education?
	Is there practical and useful knowledge about the forest that you wish to pass on?

Appendix 9: Socio-demographic characteristics of the *n* studied households in each village (**Chapter 4**).

		Malen I (n = 16)	Eschiambor (n = 39)	Mintoum (n = 78)
Total number of permanent residents		80	174	437
Native from the village		56%	65%	75%
Ethnic group	Baka	0%	0%	53%
	Bantu	100%	100%	47%
Maximum level of education	Out-of-school	0%	0%	5%
	Primary school	38%	33%	46%
	Secondary school	56%	59%	47%
	Graduate school	6%	8%	2%
Main source of income	Forest-related activities	73%	21%	53%
	Agriculture	7%	46%	10%
	Salary jobs	13%	10%	23%
	Mixed occupation	7%	23%	14%