CONSERVATION AND MONITORING OF WILDLIFE IN LOGGED TROPICAL FORESTS

A STUDY IN WESTERN EQUATORIAL AFRICA

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A study in Western Equatorial Africa

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Utrecht University
December 2022

Layout and printing: ProefschriftMaken || www.proefschriftmaken.nl

ISBN: 978-94-6469-326-3

Conservation and monitoring of wildlife in logged tropical forests

A study in Western Equatorial Africa

Behoud en monitoring van dieren in gekapte tropische bossen

Een studie in West-Equatoriaal Afrika
(met een samenvatting in het Nederlands)

Conservation et surveillance de la faune dans les forêts tropicales exploitées

Une étude en Afrique équatoriale occidentale
(avec un résumé en français)

Proefschrift

ter verkrijging van de graad van doctor aan de
Universiteit Utrecht
op gezag van de
rector magnificus, prof.dr. H.R.B.M. Kummeling,
ingevolge het besluit van het college voor promoties
in het openbaar te verdedigen op

donderdag 29 juni 2023 des middags te 4.15 uur

door

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geboren op 26 januari 1988
te Eindhoven

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Dit proefschrift werd (mede) mogelijk gemaakt met financiële steun van de Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO) via het graduate programme ‘Nature Conservation, Management and Restoration’, het Wereld Natuur Fonds (WWF), het programme de Promotion de l'Exploitation Certifiée des Forets (PPECF) en de Prins Bernhard Leerstoel voor Internationale Natuurbescherming.

– Apart from the legal requirements, cultural values, ecological interactions and economic considerations, it is above all the diversity of life, the intrinsic value of the vast uniqueness of lifeforms to which we ourselves belong, that obliges us to bridle our destructiveness and wield our inventiveness, to organize and to be ambitious in order to conserve what we can only lose but never create. –

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Summary

Tropical forests harbor the largest share of all terrestrial biodiversity, including 62% of all terrestrial vertebrate species. Of the remaining tropical forests, more than one-quarter are designated as logging concessions, potentially putting wildlife at risk. Forest certification systems like the Forest Stewardship Council (FSC) claim that they address threats to biodiversity, but studies have to date not resulted in robust verification of impacts of certified logging on wildlife communities due to limitations in research design and scale. Measuring impact is important for informed decision-making and data-driven policies. For this, reliable population monitoring is a prerequisite. In this thesis the general aims are to assess whether wildlife is more effectively conserved in FSC-certified logging concessions than in non-FSC concessions, and to explore how wildlife populations can best be monitored in tropical forests. I start this thesis by reviewing the applications of the three main monitoring methods to provide guidance on wildlife monitoring in tropical forests. Then, I examine the knowledge gap concerning the impacts of FSC-certified forestry, by assessing whether wildlife is more effectively conserved in FSC-certified logging concessions than in non-FSC concessions. The data were gathered by using camera traps in fourteen forestry concessions in Western Equatorial Africa. I found that FSC-certified forestry benefits mammals when compared to non-FSC forestry, with the most pronounced positive impacts for mammals weighing 10 kg and more. Next, I develop and test two wildlife monitoring methods: the use of sound for primate monitoring, and the use of soundscapes as a proxy for the overall biodiversity in a forest. Species-specific monitoring using sound covers a different species range than camera traps. However, sound monitoring requires automated classification for it to be useful. For soundscapes, interpretation of changes in the soundscape and quantification of individual species' contributions are the main challenges, as well as interpreting the relationship between the structure of the soundscape and local landscape heterogeneity. Further development and enhancement of wildlife monitoring methods is essential for impact verification and improvement of forest certification. Improved wildlife monitoring methods may also aid the development of biodiversity credit systems, potentially yielding new revenue streams for conservation.

Lay summary

Tropical forests contain the most biodiversity of all land areas, including 62% of all vertebrate species on land. Of the remaining tropical forests, more than one-quarter are used for selective logging for timber. This means that commercially valuable trees are cut down and extracted via a dense network of logging roads. These roads open up the forest to hunters, potentially putting wildlife at risk. Forest certification systems like the Forest Stewardship Council (FSC) claim that they reduce threats to biodiversity, but studies have to date not resulted in convincing proof that certified logging is indeed better for wildlife than non-FSC logging. Measuring and proving that management measures are indeed effective is important for informed decision-making and data-driven policies. For this, reliable population monitoring is a prerequisite.

In this thesis the general aims are to assess whether wildlife is more effectively conserved in FSC-certified logging concessions than in non-FSC concessions, and to explore how wildlife populations can best be monitored in tropical forests. I start this thesis by reviewing the applications of the three main monitoring methods to provide guidance on wildlife monitoring in tropical forests. Then, I investigate the knowledge gap concerning the impacts of FSC-certified forestry, by assessing whether wildlife is more effectively conserved in FSC-certified logging concessions than in non-FSC concessions. The data were gathered by using camera traps in fourteen forestry concessions in Western Equatorial Africa.

I found that FSC-certified forestry benefits mammals when compared to non-FSC forestry, with the most pronounced positive impacts for mammals weighing 10 kg and more. Next, I develop and test two wildlife monitoring methods: the use of sound for primate monitoring, and the use of soundscapes as a surrogate for the overall biodiversity in a forest. Monitoring individual species by using sound allows for other species to be detected than with camera traps. However, sound monitoring requires species being vocally active and automated recognition of species in the sound recordings for it to be useful. For soundscapes, the main challenge lies in interpreting what changes in soundscape mean in terms of changes in biodiversity. It is also unclear how soundscapes vary under different local circumstances and how it can be identified which species are the main contributors to the soundscape. Further development and enhancement of wildlife monitoring methods is essential for impact verification and improvement of forest certification. Improving wildlife monitoring methods may also aid the development of payments for biodiversity conservation. Such systems may help to raise new funds for conservation of wildlife in tropical forests.

Chapter 1

General introduction

The biodiversity crisis

The concept of planetary boundaries aims to visualize to what degree humans affect planet Earth. Various planetary boundaries are being crossed beyond critical levels or are in zones of uncertainty, including nitrogen and phosphorus flows to the biosphere and oceans, climate change, and land-system change, which affects the integrity and stability of the Earth system (Fig. 1; Steffen et al., 2015). Few boundaries, however, are being crossed as severely and persistently as the biosphere integrity of our planet, and likewise, few crises are as severe and persistent as the biodiversity crisis (Díaz et al., 2019). Despite global recognition of this problem, biodiversity loss is still accelerating in what is already known as the sixth mass extinction (Ceballos et al., 2015; McCallum, 2015; Sandor et al., 2022). The predominant drivers that result in biodiversity loss include habitat loss through land-use change, overexploitation, pollution, climate change and invasive species (Mazor et al., 2018).

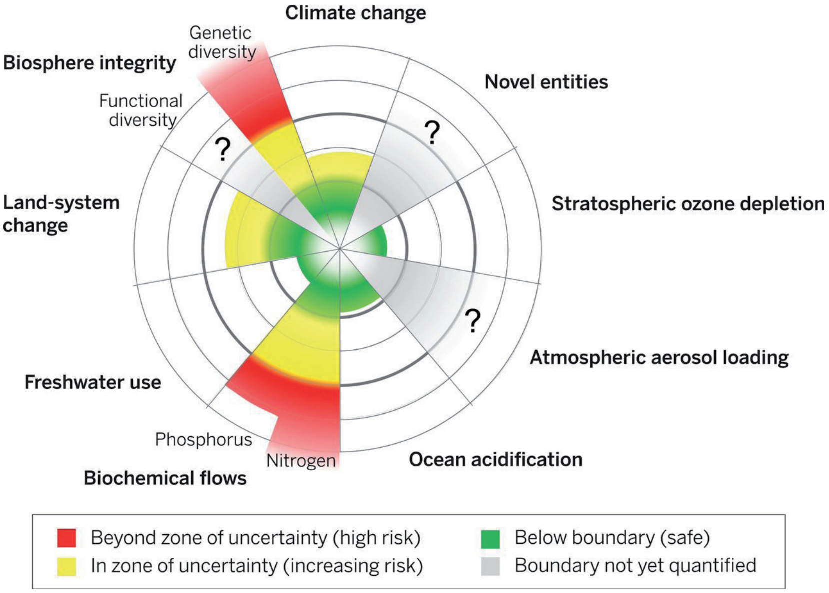

Figure 1. Current status of the control variables for seven of the planetary boundaries. The green zone is the safe operating space, the yellow represents the zone of uncertainty (increasing risk), and the red is a high-risk zone. The planetary boundary itself lies at the intersection of the green and yellow zones. The control variables have been normalized for the zone of uncertainty; the center of the figure therefore does not represent values of 0 for the control variables. The control variable shown for climate change is atmospheric CO2 concentration. Processes for which global-level boundaries cannot yet be quantified are represented by gray wedges; these are atmospheric aerosol loading, novel entities, and the functional role of biosphere integrity (Steffen et al., 2015).

Despite a detailed understanding of the underlying causes of biodiversity loss, and despite international pledges for action, *e.g.* the incorporation of biodiversity in the Sustainable Development Goals (SDGs) and multilateral treaties such as the Convention on Biological Diversity (CBD), there are but few effective solutions to mitigate the loss of biodiversity (Baste et al., 2021; Bolam et al., 2021; Johnson et al., 2017).

Tropical forests, the most biodiverse biome of the planet, are principally affected by land-use change and between 2011 and 2020, have been deforested at a rate of 3.6 to 8.8 million hectares per year (Curtis et al., 2018; FAO, 2022b; Hoang & Kanemoto, 2021; Pendrill et al., 2022). Each of the planet's three large tropical forest regions (in Southeast Asia, Amazonia, and Central Africa) is affected by the production of different agro-industrial commodities (Goldman et al., 2020; Pendrill et al., 2022) (Box 1). In Asia most deforestation is driven by palm oil production (Vijay et al., 2016), while South American forests are predominantly converted for cattle ranching and soybean farming (Barona et al., 2010; Dos Santos et al., 2021). West African forests are mainly affected by cocoa production, which is increasingly expanding into Central African forests (Goldman et al., 2020). Tropical forests are also increasingly degraded and fragmented, primarily through infrastructure development, defaunation, forest fires, and illegal and unsustainable logging (Dirzo et al., 2014; Potapov et al., 2017; Venter et al., 2016; Wilkie et al., 2011). The loss and degradation of tropical forests affects vast numbers of species; of the 25,000 species that are currently listed as endangered or critically endangered on the IUCN Red List, approximately 14,000 species inhabit tropical forests (IUCN, 2022).

Protected areas are part of the solution to counteract biodiversity loss. However, they are too small to sustain much of the wildlife that still exists today (Maxwell et al., 2020;

Box 1. A shared responsibility

A common paradigm in the Global North is that forested nations should put a halt to deforestation of biodiversity and carbon rich tropical forests. Indignation about the destruction of tropical forests, however, is somewhat misplaced and requires nuance. The economic development of countries in the Global North went alongside with the destruction of its forests and ecosystems, while many nations in the tropics retained their forests. These forest rich nations are now developing their agro-industries, largely fueled by demand from the Global North (Hoang and Kanemoto 2021). The resulting land-use change for the production of commodities and connected destruction of tropical forests is likely to continue unless realistic economically sustainable alternatives are developed and upscaled. Therefore, the conservation of tropical forests can be considered a shared responsibility.

Watson et al., 2014). For example, chimpanzees and gorillas have an approximate 87% of their combined ranges outside of national parks (Strindberg et al., 2018), with similar numbers for other forest dwelling species. Moreover, protected areas are too fragmented to allow for effective long-term conservation (Brennan et al., 2022; Ward et al., 2020). The lack of connectivity prevents animal movement and migration (Harris et al., 2009; Tucker et al., 2018), resulting in loss of genetic diversity and associated extinction vortexes (Fagan & Holmes, 2006). Finally, managing and patrolling protected areas is costly and requires substantial and stable financing (Lindsey et al., 2021; Lindsey et al., 2017). Many tropical forests are situated in countries with developing economies which lack such resources (OECD 2019). A lack of funding can lead to ineffective management, and indeed, there are many examples of illegal activities (Harrison, 2011; Poulsen et al., 2017) and even deforestation in protected areas (Curran et al., 2004; Laurance et al., 2012; Leberger et al., 2020; Spracklen et al., 2015; Wade et al., 2020). Additionally, protecting forests incurs substantial opportunity costs, as retaining a forest prohibits the development of more economically rewarding activities (Carwardine et al., 2008; Ceballos et al., 2005; Schröter et al., 2014; Venter et al., 2009). In certain contexts, funding can be secured by revenue from ecotourism (Krüger, 2005), but tropical forests are less suitable for large scale tourism over extended areas as they present comparatively few opportunities to encounter iconic wildlife, can be uncomfortable, difficult to reach, and although they are highly biodiverse, they can appear relatively homogenous for the casual observer (Wilkie & Carpenter, 1999). Thus, designating forested land for conservation alone is not a realistic option to curb the biodiversity crisis. Alternative ways to protect tropical forests and their wildlife need to be considered as well.

Selective logging

One approach to add value to standing tropical forests, and thereby to prevent forest conversion for agro-industrial commodities, is by harvesting timber through selective logging. Tropical forests are highly diverse and contain over 40,000 tree species worldwide (Slik et al., 2015). Many tropical tree species do not have desirable wood properties, which necessitates selectively harvesting economically interesting species that tend to have dense wood and relatively slow growth rates. Harvesting tropical hardwoods in a selective manner allows for most of the forests to be retained and is therefore assumed to largely preserve forest habitats and its wildlife. Target trees are prospected, marked, felled and then extracted by skidders. For these operations, a network of primary and secondary roads is created that branch off into logging trails. Logging concessions are typically exploited over 25 to 30-year cycles, whereby the concession is divided into annual cutting blocks that are logged only once per cycle.

Box 2. Elephants and climate: carbon calculations on the back of an envelope
African forest elephants weed out small trees, which alleviates the competition for resources for other trees, allowing them to grow larger and store more carbon. Through this mechanism alone, it has been calculated that Central African forests will in the long run store 7% less carbon if forest elephants go extinct (Berzaghi et al. 2019). Given that African tropical forests store an approximate 183 tons of carbon per hectare (Sullivan et al., 2017), a 7% loss would entail a reduction of 13 tons per hectare. For 220 million hectares of African tropical forest where elephants could potentially roam, this amounts to 2.9 Gt less CO_2, which surpasses the entire annual emissions of India. At a conservative carbon price of €15 per ton CO_2, this implies that protecting and preserving elephants alone already results in a climate benefit through carbon storage of €42.9 billion

From a nature conservation perspective, selective logging may be a relatively benign form of land-use, because most of the forest is retained – in Western Equatorial Africa often only two to four trees per hectare are extracted – whilst the timber producing countries benefit economically. However, forestry involves bringing and settling workers and their families in remote, often newly created settlements in the heart of previously very remote areas. Moreover, the extensive road networks created to extract the logs from the forest bring along a range of indirect effects, including illegal settlement, mining, increased forest fires, deforestation and hunting (Barber et al., 2014; Laurance et al., 2009). Regarding hunting for instance, a person can walk approximately 10 km per day in a tropical forest, which limits the area that is affected by hunters (Froese et al., 2022). With increased accessibility from roads, the potential hunting area is greatly increased (Benítez-López et al., 2017; Kleinschroth & Healey, 2017). Such negative impacts are highly detrimental to the wildlife living in these forests, and as logging concessions cover more than 400 million hectares of tropical forests, or roughly an area twice the size of Mexico (Blaser et al., 2011), these are important issues that need to be addressed.

Wildlife

Tropical forests harbor over 62% of all terrestrial vertebrates, of which 29% are endemic and more than 20% are at risk of extinction (Pillay et al., 2022). Wildlife plays a pivotal role in forest ecosystems and their loss affects complex ecological networks and processes such as seed dispersal, seed predation, browsing, plant competition, nutrient cycling, predation, and modification of the vegetation structure (Abernethy et al., 2013; Rogers et al., 2021). Medium- to large-sized mammals are involved in processes that affect the forest carbon storage potential through dispersion and predation of large seeds (Beaune et al., 2013; Bello et al., 2015; Chanthorn et al., 2019; Peres et al., 2016), turnover of small trees (Berzaghi et al., 2019), and herbivory of fast-growing plants (Poulsen et al., 2013; Vaessen et al., 2022). Losing these functions allows low wood density plants to proliferate at the cost of high wood density trees that store more carbon, which results in less carbon stored per hectare of forest (Box 2). Degraded wildlife communities may furthermore increase the chance of future pandemics, as lower biodiversity and high relative prevalence of rodents in impoverished ecosystems are both associated with increased zoonotic disease transmission (Johnson et al., 2020). Forest wildlife also has an important role in providing proteins to rural human communities in forested regions. However, wildlife populations are being reduced to the point that the long-term protein provisioning function in local rural areas is at risk (Cawthorn & Hoffman, 2015; Nasi & Fa, 2015). Apart from a functional perspective, wildlife also represents immense intrinsic value, as they are unique living beings in the intricate web of life and are worthy of our ambitions and our efforts to protect them from humans (Vucetich et al., 2015).

Forest certification

To prevent forest degradation and to preserve biodiversity, the undesirable consequences of extensive infrastructure and human activity resulting from logging in previously remote areas need to be managed (Kleinschroth et al., 2019). In 1993, the Forest Stewardship Council (FSC) was created as a voluntary and independent member organization that aims to promote environmentally sound, socially beneficial, and economically viable management of the world's forests (Perera & Vlosky, 2006). Subsequently, other certification standards were created, such as the Programme for the Endorsement of Forest Certification (PEFC). In this thesis, I focus on FSC-certified forestry only, as FSC is widely considered as the most rigorous certification scheme (Gutierrez Garzon et al., 2020; Judge-Lord et al., 2020).

Forestry companies can become FSC-certified if they adhere to FSC's 10 principles (FSC, 2015: Box 3). These principles and criteria have global applicability, but are adapted to regional and national contexts with locally relevant indicators for verification of compliance. To ensure that all principles are respected, FSC-certified companies are audited by independent third-party companies. FSC's members consist of a large variety of stakeholders, including businesses, environmental and social NGOs, and interested individuals. Every three years, a general assembly is held where members can propose motions to adapt FSC's regulations. The FSC is governed by a three-chamber system; the economic, social, and environmental chamber, each with equal voting power regarding proposed motions to modify the system. A motion requires a majority vote of each of the three chambers in order to pass, ensuring that all requirements are economically, socially, and environmentally responsible. Within each chamber, votes are weighed across the members from the Northern and Southern hemispheres, to ensure influence is shared equitably between interest groups and countries with different levels of economic development.

In the social domain, FSC addresses among other things: workers' rights, safety regulations, benefit-sharing with neighboring communities, and protection of indigenous peoples' rights (Cerutti et al., 2014). Environmental FSC requirements include protection of vulnerable ecosystems, species and ecosystem services, prohibition of illegal hunting, regular wildlife monitoring, strict adherence to national law, and implementation of management plans. Management plans include a wide variety of measures to prevent illegal hunting and bushmeat trafficking, such as the closing of old logging roads, having manned barriers on primary roads in the concession, prohibiting the transport of hunting materials or bushmeat in company vehicles, the provision of alternative proteins to workers and their families in logging camps, and anti-poaching patrols (Clark & Poulsen, 2012).

Although there is convincing evidence that FSC certification has resulted in positive social impacts (Cerutti et al., 2014), there is less evidence that FSC's environmental requirements are effective; the few existing studies' limited geographic scale and in-study degree of replication have hindered a deeper understanding of impacts. Demonstrating environmental impacts is essential to uphold the credibility of the system; this is especially pertinent given the investments by both timber producers and consumers. Positive environmental effects have been demonstrated for single concessions (Sollmann et al., 2017), or for one or two mammal species such as jaguars (Polisar et al., 2017) and forest elephants and great apes (Stokes et al., 2010), but no studies have yet assessed the whole mammal community in a well replicated design (Burivalova et al., 2017; van der Ven & Cashore, 2018). The lack of replication is a common problem in landscape scale ecological studies (Ramage et al., 2013), as replication of large sampling units is costly, logistically challenging, complex due to landscape heterogeneity, and proper controls are often lacking. This replication problem also applies to forestry concessions, as they cover extensive areas, which complicates making valid comparisons between the effectiveness of forest management types. Nonetheless, replication of sites is essential to be able to attribute differences in wildlife abundance to a type of management over the influence of location, history, or chance. For instance, the influence of a neighboring protected area adjacent to one concession but not to another could confound the effect of management type, ultimately resulting in incorrect conclusions about the impact of a management regime.

Box 3. The 10 Principles of the Forest Stewardship Council (FSC, 2015)

Principle 1: Compliance with Laws

The Organisation shall comply with all applicable laws, regulations and nationally ratified international treaties, conventions, and agreements.

Principle 2: Workers' Rights and Employment Conditions

The Organisation shall maintain or enhance the social and economic wellbeing of workers.

Principle 3: Indigenous Peoples' Rights

The Organisation shall identify and uphold Indigenous Peoples' legal and customary rights of ownership, use and management of land, territories and resources affected by management activities.

Principle 4: Community Relations

The Organisation shall contribute to maintaining or enhancing the social and economic wellbeing of local communities.

Principle 5: Benefits from the Forest

The Organisation shall efficiently manage the range of multiple products and services of the Management Unit to maintain or enhance long term economic viability and the range of environmental and social benefits.

Principle 6: Environmental Values and Impacts

The Organisation shall maintain, conserve and/or restore ecosystem services and environmental values of the Management Unit, and shall avoid, repair, or mitigate negative environmental impacts.

Principle 7: Management Planning

The Organisation shall have a management plan consistent with its policies and objectives and proportionate to scale, intensity and risks of its management activities. The management plan shall be implemented and kept up to date based on monitoring information to promote adaptive management. The associated planning and procedural documentation shall be sufficient to guide staff, inform affected stakeholders and interested stakeholders and to justify management decisions.

Principle 8: Monitoring and Assessment

The Organisation shall demonstrate that, progress towards achieving the management objectives, the impacts of management activities and the condition of the Management Unit, are monitored and evaluated proportionate to the scale, intensity, and risk of management activities, to implement adaptive management.

Principle 9: High Conservation Values

The Organisation shall maintain and/or enhance the High Conservation Values in the Management Unit through applying the precautionary approach.

Principle 10: Implementation of Management Activities

Management activities conducted by or for The Organisation for the Management Unit shall be selected and implemented consistent with The Organisation's economic, environmental, and social policies and objectives and in compliance with the Principles and Criteria collectively.

To study whether wildlife is better protected in FSC-certified concessions than in non-FSC concessions, it is important to include as many species as possible. The ecology and behavior of each species are unique, and species may therefore respond differently to the type of conservation measures typically associated with FSC management. For example, gorillas and chimpanzees react differently to the presence of roads, even though they are closely related. Gorillas have been found to benefit more from roads with anti-poaching patrols than chimpanzees (Strindberg et al., 2018). This is because gorillas are more folivorous than chimpanzees and are therefore attracted to roads, where disturbance allows for the growth of fast growing and palatable plants, whereas chimpanzees rely more on fruits in the forest interior. Moreover, gorillas are more vulnerable to hunting, as males stand guard to protect their family and therefore form easy targets for armed hunters. If the alpha male dies, a new alpha male often commits infanticide, further exacerbating the effect of hunting (Robbins & Robbins, 2018). Due to this type of species-specific responses, monitoring the distribution and abundance of only one or a few species may provide a distorted image of the effect of forest management and conservation measures on the wildlife community.

Wildlife monitoring

To measure the impacts of forest certification or other management approaches on wildlife populations, cost-effective wildlife monitoring methods are required. There is not one single method that can be used to monitor all species effectively, necessitating an integrated approach of multiple methods for a complete view of the wildlife community. Traditional monitoring in tropical forests has relied mostly on human observations, which focuses on common species that are either visible during the day or produce signs with a known production and decay rate that can be counted (essentially elephant and ungulate dung, and ape nests). Over the last two decades, motion triggered camera traps have increasingly been used for wildlife monitoring in tropical forests (Glover-Kapfer et al., 2019). They have the advantage that they can be left in the field for extended periods of time, are non-invasive, and are able to record a wide range of species. The use of sound recorders, or Passive Acoustic Monitoring (PAM), is also increasingly being used for wildlife monitoring, albeit less frequently than camera traps (Darras et al., 2019). One advantage of PAM is that it has a different detection range than camera traps, allowing for instance for the monitoring of arboreal wildlife. PAM data can, like camera trap data, also be used to assess abundance, activity patterns, and in some cases also sex, behavior, individually recognizable animals, and even the emotional state of individuals (Enari et al., 2019; Mielke & Zuberbühler, 2013; Soltis et al., 2005).

PAM can also be used for soundscape ecological studies which examine the overall acoustic complexity of an ecosystem, using an expanding library of acoustic indices that relate the intensity of sound activity to wildlife diversity or abundance (Aide et al., 2017; Buxton et al., 2018; Scarpelli et al., 2020; Sueur et al., 2014). Such acoustic proxies for biodiversity have the advantage of capturing all acoustically active biodiversity, providing a broader image of the biodiversity in an ecosystem and including taxa that are poorly monitored by other methods, such as insects and amphibians (Aide et al., 2017; Troudet et al., 2017). Soundscape studies can for instance be used to detect and quantify anthropogenic impacts on biodiversity (Burivalova et al., 2018; Campos-Cerqueira et al., 2019; Deichmann et al., 2017).

More species can be monitored using camera traps and sound recorders than by human observers and both methods easily gather vast amounts of data. Labelling and interpreting these data to quantify species observations requires considerable time; much progress can be made by further automating these processes. The further development of cost-effective monitoring methods is vital in order to understand the impacts of certified forest management and related conservation measures on wildlife populations, which is essential for effective wildlife conservation.

Study area

The data for this research were collected in the Republic of Congo and in Gabon. These countries are located in West Equatorial Africa, which is part of the second largest tropical forest on the planet. Much remains to be conserved in these forests, both in terms of forest extent (Grantham et al., 2020; Potapov et al., 2017) and in terms of wildlife (Plumptre et al., 2021). Together, the Republic of Congo and Gabon hold about 70% of forest elephants and almost 90% of western gorillas, despite holding only about a quarter of Central Africa's total forest cover (Maisels et al., 2013; Strindberg et al., 2018). In 2020, 14.5% of the forests of Gabon were protected; 91.3% of the land was covered by forest. In Congo, 17.8% was protected and 64.2% of the land area was covered by forest (FAO, 2022a). All forests in the region are owned by the state and the majority are designated as logging concessions; roughly 4.5 times more land is allocated for logging than for conservation in both Congo and Gabon (Eba'a Atyi et al., 2022). Logging is done in 25-year cycles and extracted volumes per hectare are low with an approximate 4 to 8 m^3 extracted timber per hectare (Karsenty, 2016). Deforestation is relatively low, as human populations are relatively small and economies have traditionally been more dependent on oil and mineral exploitation than on agricultural expansion, the former being far more localized and less impactful on forest extent than the latter. Rural populations in the region predominantly practice slash and burn subsistence farming. Countries in Western Equatorial Africa are increasingly urbanized and now have more people living in cities than in the rural areas (World bank, 2022). This spurs an increasing demand for bushmeat from urban populations, which in combination with increased accessibility of tropical forests has over the last decades culminated in the "bushmeat crisis", whereby wild meat is extracted in unsustainable volumes from tropical forests and traded in distant markets either for meat or other body parts (Abernethy et al., 2016; Abernethy et al., 2013; Benítez-López et al., 2017; Nasi et al., 2008; Wilkie et al., 2011). Both countries harbor multiple FCS-certified and non-FSC logging concessions, providing an ideal setting for a systematic and controlled establishment of the environmental effects of FSC certification.

Guide to the reader

This thesis investigates the conservation and monitoring of wildlife in logged tropical forests. The general aims are to assess whether wildlife is more effectively conserved in FSC-certified logging concessions than in non-FSC concessions, and to explore how wildlife populations can best be monitored in tropical forests. The societal relevance of this study entails developing knowledge and methods needed for wildlife conservation in logged tropical forests. As the global human population increasingly requires resources (Elhacham et al., 2020), it is essential that these resources are produced responsibly. Producing sustainable and responsible natural resources while facilitating biodiversity conservation connects to SDG 12 Responsible Consumption and Production and SDG 15 Life on Land. The question that initiated this PhD research was whether FSC-certified forestry is effective in conserving wildlife, compared to non-FSC. In order to answer this question, I discuss how to best monitor wildlife by reviewing common and new monitoring techniques in chapter 2. The effectiveness of FSC-certified forestry compared to non-FSC is then assessed in chapter 3 by means of the use of camera traps. The use of acoustic monitoring is rapidly increasing, but still requires methodological improvements for large-scale application and mainstream adoption. For species specific recognition this is discussed in chapter 4, and for the use of soundscapes in chapter 5.

Chapter 2 - To evaluate the effectiveness of conservation approaches, cost-effective monitoring methods are required. The monitoring methods most commonly used in tropical forests are direct observations made by humans (visual or acoustic), camera traps, or passive acoustic sensors. Each monitoring method is suitable for certain (groups of) species and each has its respective limitations. Knowledge of the advantages and disadvantages of these methods is important for appropriate method selection and to stimulate multi-method approaches for wildlife monitoring. To facilitate effective and goal-oriented monitoring by scientists and practitioners (e.g., the private sector, government agencies, and NGOs), we extensively review these methods in chapter 2 in relation to four important aspects that need to be considered before starting monitoring programs: (1) targetable species, (2) attainability of population metrics and precision, (3) required expertise, tools and effort for species identification, and (4) required financial and human resources.

Chapter 3 - To conserve wildlife in tropical forests in the decades to come, forests need to be managed responsibly. FSC claims to do this by reducing the direct and indirect negative impact of forestry. It has however not been robustly established whether FSC-certified management indeed effectuates the desired environmental results and this knowledge gap needs to be addressed. Therefore, chapter 3 addresses whether FSC-certified forestry concessions effectively conserve wildlife, as opposed to conventional logging concessions.

Chapter 4 - Wildlife monitoring is expensive and complex, and impact evaluations are often ignored in project planning. By reducing costs, increasing species coverage, and increasing efficiency of monitoring methods, monitoring can be made more accessible, precise and effective. For this, wildlife monitoring methods need to be developed, improved and automated. To monitor species acoustically, it is essential that the detection of target sounds becomes automated, as manually listening to audio recordings is too time-inefficient for any large-scale monitoring project. In chapter 4, I contribute to the automation of acoustic detection of primates by developing a new set of detection algorithms.

Chapter 5 - Large and iconic wildlife species tend to have the highest conservation priority, but gathering information about smaller species can also provide valuable insights into ecosystem dynamics and anthropogenic impacts (Burivalova et al., 2018). Therefore, apart from species-specific monitoring, soundscapes can be used as a proxy for overall biodiversity of an ecosystem. This relatively new approach for biodiversity monitoring remains difficult to interpret without a better understanding of how soundscapes are influenced by heterogeneity in the landscape (Sueur & Farina, 2015). To increase our ability to interpret soundscapes and to further develop the application of soundscape monitoring, I explore 5 how soundscapes are influenced by landscape heterogeneity and how they relate to observations recorded by camera traps in chapter 5.

Chapter 6 – In the final chapter, all findings are synthesized and discussed in relation to developments in wildlife conservation. This includes perspectives on the role of automation, legislation and the potential for biodiversity credits.

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Elephants are curious animals, sometimes a bit too curious.

Chapter 2

Methods for wildlife monitoring in tropical forests: Comparing human observations, camera traps and passive acoustic sensors

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This chapter has been published in the journal Conservation Science and Practice as: Zwerts, J. A., Stephenson, P. J., Maisels, F., Rowcliffe, M., Astaras, C., Jansen, P. A., van Der Waarde, J., Sterck, L. E. H. M., Verweij, P. A., Bruce, T., & van Kuijk, M. (2021). Methods for wildlife monitoring in tropical forests: Comparing human observations, camera traps, and passive acoustic sensors. *Conservation Science and Practice*, *3*(12), e568. https://doi.org/10.1111/csp2.568

Abstract

Wildlife monitoring is essential for conservation science and data-driven decision-making. Tropical forests pose a particularly challenging environment for monitoring wildlife due to the dense vegetation, and diverse and cryptic species with relatively low abundances. The most commonly used monitoring methods in tropical forests are observations made by humans (visual or acoustic), camera traps, or passive acoustic sensors. These methods come with trade-offs in terms of species coverage, accuracy and precision of population metrics, available technical expertise, and costs. Yet, there are no reviews that compare the characteristics of these methods in detail. Here, we comprehensively review the advantages and limitations of the three mentioned methods, by asking four key questions that are always important in relation to wildlife monitoring: (1) What are the target species? (2) Which population metrics are desirable and attainable? (3) What expertise, tools and effort are required for species identification? and (4) Which financial and human resources are required for data collection and processing? Given the diversity of monitoring objectives and circumstances, we do not aim to conclusively prescribe particular methods for all situations. Neither do we claim that any one method is superior to others. Rather, our review aims to support scientists and conservation practitioners in understanding the options and criteria that must be considered in choosing the appropriate method, given the objectives of their wildlife monitoring efforts and resources available. We focus on tropical forests because of their high conservation priority, although the information put forward is also relevant for other biomes.

Introduction

Monitoring wildlife is an essential component of conservation (CMP 2020; Nichols & Williams, 2006; Salafsky et al., 2001). Evidence-based conservation efforts, data-driven decision making for adaptive management, and sustainable use of natural resources, are all based on the premise that population declines can be detected in a timely manner (e.g. Díaz et al., 2020; Grooten & Almond, 2018). Monitoring objectives can range from assessing species presence/absence, to knowing the exact density of one or more species. Monitoring data are used across multiple scales, from local (site-level) to national, regional, and global scales (e.g. as indicators for global biodiversity goals, the IUCN Red List of Threatened Species, the CITES Appendix status of taxa, and to formulate species-specific IUCN Action Plans) (Brooks et al., 2015; IUCN, 2020; Pereira et al., 2013; Stephenson, 2019).

Tropical forests harbor a large proportion of the world's terrestrial wildlife (Myers et al., 2000). At the same time, tropical forests are a particularly challenging environment for wildlife monitoring, due to limited visibility in often dense understory, and the diverse, cryptic nature and low densities of many animal species. The complex nature of tropical forests comes with low and variable detection probability (Sollmann et al., 2013), risk of bias related to the timing and location of observations (Cusack et al., 2015), the effort required for species identification, and the cost of data collection. As each monitoring method has its advantages and limitations, and resources are often limited, it can be complicated to select a suitable monitoring method (Stephenson, 2020; Stephenson et al., 2020).

The most commonly used monitoring methods in tropical forests are direct observations made by humans (visual or acoustic), camera traps, or passive acoustic sensors. Observations by humans of wildlife or their signs have traditionally been the most commonly used method (Heyer et al., 2014; Plumptre, 2000; Sutherland, 2008; Wilson et al., 1996), but is increasingly being replaced by the use of autonomous recorders (Mulatu et al., 2017). Camera traps are now a well-established monitoring tool (Beaudrot et al., 2016; Rovero & Zimmermann, 2016) and the use of acoustic sensors for passive acoustic monitoring (PAM) is growing fast (Alvarez-Berríos et al., 2016; Blumstein et al., 2011; Deichmann et al., 2018; Sugai et al., 2019). Standardized protocols are available for human observations (Sutherland, 2008, White & Edwards 2000), camera traps (Kays et al., 2020; Meek et al., 2014; Rovero & Zimmermann, 2016; Scotson et al., 2017, Wearn et al., 2017), and PAM (Abrahams, 2018; Browning et al., 2017; Darras et al., 2018). There is also much literature comparing the outcomes of particular methods (e.g. human observation versus camera trapping: Bessone et al., 2020, Cappelle et al., 2019, Greene et al., 2016; Joshi et al., 2020, Roberts et al., 2011). However, few papers compare all three field methods (Wrege et al., 2017, Stephenson, 2020), and none do so in depth.

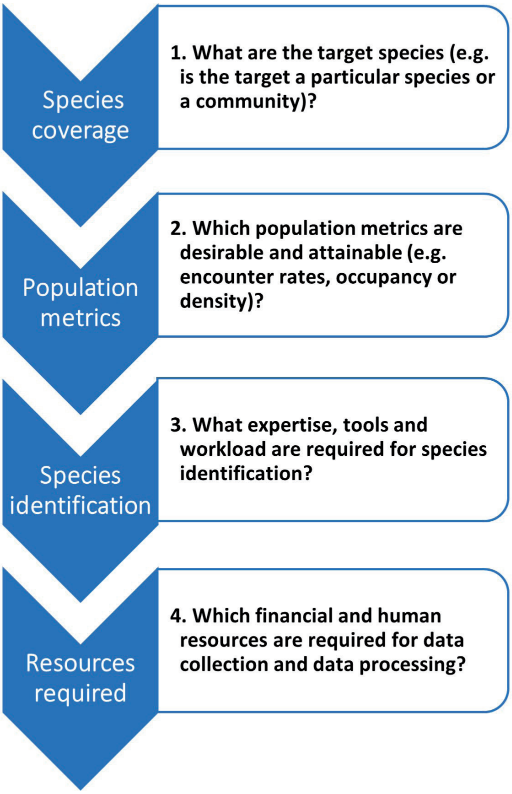
Here, we review the advantages and limitations of the three mentioned methods – observations by humans, camera traps and passive acoustic sensors – for wildlife monitoring with a focus on tropical forests given their high conservation priority, although the information we provide is also applicable in other biomes. The methods considered typically target terrestrial vertebrate wildlife, but we also consider application to invertebrates where relevant. Our aim is to objectively facilitate the correct uptake and use of these field methods for effective, goal-oriented monitoring by scientists and practitioners (e.g. the private sector, government agencies and NGOs). We evaluate each method by asking four key questions (Figure 1), that we believe need to be addressed before any monitoring survey: 1. What are the target species (e.g. is the target a community or a particular species)?; 2. Which population metrics are desirable and attainable (e.g. encounter rates, occupancy or density)?; 3. What expertise, tools and effort are required for species identification?; and 4. Which financial and human resources are required for data collection and data processing? Following these four questions, all relevant characteristics of each method are summarized in Table 1.

1. Species coverage

Every wildlife monitoring project foremost requires a clear objective with regard to its target species. Is the goal to monitor populations of particular species, or to monitor a community? Monitoring approaches differ strongly in species coverage – the number and types of species that can be detected – as well as detection biases. For species-level monitoring, the major challenge is the acquisition of sufficient data for acceptable accuracy and precision, within a manageable time and budget. A community-wide assessment requires an approach with broad and unbiased species coverage, where differences in detection probability can be estimated and accounted for.

1.1 Human observation

Observations by humans can be direct, e.g., spotting animals, or indirect, e.g., recording signs such as nests, tracks or feces (Buckland et al., 2001; 2010; Laing et al., 2003). Direct observations are biased towards mammals and birds that are easy to detect because of vocalization, size and diurnal habits, while rare, small, fossorial, nocturnal and cryptic species are less likely to be observed (Richard-Hansen et al., 2015). The likelihood of detection may vary across the day and across seasons (Pearse et al., 2015), and by shyness and habituation – animals may be repelled or attracted by observers (Marini et al., 2009; Thomas et al., 2010). Direct observation furthermore



1. What are the target species (e.g. is the target a particular species or a community)?

2. Which population metrics are desirable and attainable (e.g. encounter rates, occupancy or density)?

3. What expertise, tools and workload are required for species identification?

4. Which financial and human resources are required for data collection and data processing?

Figure 1. This review is structured along four key questions that we believe need to be considered when choosing a monitoring method.

requires highly skilled observers. Observer bias may arise from differences in skills between observers and fatigue, although these problems can be reduced by careful training, limiting the length of monitoring sessions and limiting the number of tasks assigned to each observer (Emlen & DeJong, 1992; Kühl et al., 2008). Due to these biases, direct field observations are generally most suitable for highly detectable species, rather than for community assessments that require broad taxonomic coverage (Roberts, 2011).

Indirect observations have the advantage that signs are immobile and more abundant than the animals that produce them because they remain visible for extended periods (up to several months). Detectability is less influenced by the time of day of the survey than direct animals observations. To estimate a population size from signs, the production and the decay rate of the signs need to be known (Hedges et al., 2012; Laing et al., 2003). These rates can differ across sites and seasons. For example, the decay rates of gorilla and chimpanzee nests depend on forest type, nest height and structure, and above all, precipitation (Morgan et al., 2016). The decay rates of signs should thus be estimated in the same survey area and season (Laing et al., 2003; Morgan et al., 2016), which may involve substantial effort and costs (Kuehl et al., 2007). Production rates of signs are less variable, hence estimates from similar or nearby sites can be used (e.g. Theuerkauf & Gula 2010). For signs such as footprints or markings left on trees, the rate of production and decay cannot be estimated, so only presence and occupancy estimates, but not density estimation is possible (section 2.2 and 2.3, respectively). Not all species produce signs that allow for species-specific identification (Furuichi et al., 1997; Miller et al., 2011). Genetic diagnostics, which are gaining in importance, can help in this case, even for identifying individuals, although this adds costs and complexity (Bowkett et al., 2009; Gray et al., 2013). Many species, such as most felids, do not leave sufficient species-specific signs with known production and decay rates for robust population estimates, and therefore require other monitoring methods (Borah et al., 2014).

Observations can be made either on line, point or reconnaissance transects (recces) (Hedges et al., 2012). Line or point transects are predefined randomly located straight lines or points from which observations are made, allowing for distance measurements to the observed objects required for density estimation with distance sampling (section 2.3). Recces are transects that follow a path of least resistance, i.e. the easiest path to follow, without the possibility of collecting additional parameters such as distance from the transect, and can therefore only be used for encounter rates or occupancy analyses (section 2.1 and 2.2 respectively).

1.2 Camera trapping

The use of camera trapping has increased rapidly over the past two decades (Glover-Kapfer et al., 2019; Wearn & Glover-Kapfer, 2017). Triggered by passive infra-red sensors (Welbourne et al., 2016), camera traps record wildlife of a broad array of size classes and taxonomic groups, including mammals (Tobler et al., 2008), birds (O'Brien & Kinnaird, 2008), and reptiles (Richardson et al., 2018), with minimal invasiveness. With time-lapse photography or specialized camera traps, even arthropods can be surveyed (e.g. Collett & Fisher, 2017; Hobbs & Brehme, 2017). Camera trapping is generally most effective for medium to large terrestrial animals, but can also be used to survey smaller, cryptic and rare animals that typically go undetected by humans (Bessone et al., 2020, Glen et al., 2013; Khwaja et al., 2019). Because camera traps record continuously and automatically, they are not biased by the timing of activity of the target species or observer skill or fatigue, making the collection process more standardized and transparent than with human observations. Also, every observation comes with a photograph that can be used for verification and validation. Additionally, as each observation is timestamped, camera trapping informs about activity patterns and human disturbance (Caravaggi et al., 2017; Gaynor et al., 2018; Ramirez et al., 2021).

A camera trap covers only a small surface area (typically 10-20 m^2). This, coupled with non-random use of space by wildlife, makes it particularly important to carefully consider study design and placement strategy (e.g. spacing and location in relation to trails or streams). When surveying target species, detections can be boosted by placing cameras at locations known to be frequented (Cusack et al., 2015; Harmsen et al., 2010; Kolowski & Forrester, 2017) or by using lures or baits (Mills et al., 2019; du Preez et al., 2014). While this strategy can work when coupled with appropriate analytical methods that control for variation in detection (covered in section 2.1), it must be recognized that boosting detectability for one species may have unpredictable effects on the detectability of others (Kolowski & Forrester, 2017). For example, while dominant predators may preferentially travel along larger trails (Karanth, 1995), many prey species, as well as competitor species and even subdominant individuals of the same species, may avoid these landscape features as a result (Wearn & Glover-Kapfer 2019).

When surveying a wildlife community, it is vital that cameras are installed at randomized locations with respect to local landscape features. Such a survey design may take the form of a systematic grid of points with a randomly allocated starting position (*e.g.* the TEAM protocol; Jansen et al., 2014), which is also essential when density estimation for non-individually recognizable individuals is planned (section 2.3), and can be stratified by habitat type if desired. The mounting height also influences the community that is effectively sampled. This happens most strongly through the exclusion of fully arboreal species with terrestrial placements, but small terrestrial species get excluded as the camera is mounted further from the ground. While canopy wildlife has effectively been studied with camera traps (Gregory et al., 2014; Moore et al., 2020; Whitworth et al., 2016), the difficulty and danger of placing camera traps in the canopy may preclude this approach for most monitoring projects.

1.3 Passive Acoustic Monitoring

Passive acoustic monitoring (PAM) uses acoustic sensors, often referred to as Autonomous Recording Units (ARU), to survey wildlife by recording vocalizations and other species-specific sounds. PAM is rapidly growing as monitoring method for terrestrial wildlife (Darras et al., 2019), in addition to marine environments where it is commonly used for monitoring cetaceans. ARUs record – often continuously and for extended periods of time – the soundscape of a given area, i.e. all sounds measured as frequency and intensity over time, consisting of biotic (e.g. animals), abiotic (e.g. rain, wind) and anthropogenic (e.g. vehicle traffic) sounds (Pijanowski et al., 2011). All species that produce identifiable calls (e.g. elephants trumpeting or rumbling; Wrege et al., 2017) or sounds (e.g. chimpanzees buttress drumming, gorillas chest beating; Heinicke et al., 2015) can be monitored with PAM, including many taxa that are poorly captured by other methods, such as insects (Ganchev & Potamitis, 2007) and amphibians (Aide et al., 2017; Troudet et al., 2017). Bats (Russo & Voigt, 2016) are the taxon most often monitored using PAM, followed by birds (Brandes, 2008) and anuran amphibians (Brauer et al., 2016; Sugai et al., 2019).

Acoustic recordings are typically used to monitor species presence and activity patterns, but in some cases also the sex, behavior, individuals and even emotional state of individuals can be deduced (Mielke & Zuberbühler, 2013; Soltis et al., 2005). For most species, the detection area of ARUs is much larger than that of camera traps (Diggins et al., 2016; Enari et al., 2019) and therefore the precise installation location introduces less bias in terms of the species that can be detected. Since the loudness of calls affects the effective survey area of ARUs (Hutto & Stutzman, 2009), comparing detection rates across species is only possible when the detection range for each species is known (section 2.1). Detections of focal species can, as with camera traps, be maximized by deploying ARUs near landscape features frequented by wildlife such as mineral licks or nesting sites, or by recording during seasons with high calling activity by the target species (e.g. breeding season). Such recording protocols should be standardized however across sites, and potential variability in detection probability accounted for, if abundance trends over space or time are to be reliably inferred.

Like camera traps, ARUs can monitor continuously, enabling the study of temporal vocal activity patterns (Sugai et al., 2019), even in periods and areas where it is logistically challenging to do field observations. The accuracy of PAM estimates, however, varies widely with species, distance to recorders and ambient noise levels, precluding absolute abundance estimates for most species (Brauer et al., 2016; Stowell et al., 2019). Moreover, estimating the number of individuals in group-living species is problematic, as counting simultaneously vocalizing individuals is difficult (Sedláček et al., 2015). Furthermore, the calls of quieter species, such as many mammals, may be swamped by more vocal species. This is especially the case during sound-rich moments such as the dawn and dusk (Hutto & Stutzman, 2009). Comparative studies reported a large overlap in bird species richness estimates between PAM and human field observations, with each method also detecting unique species (Darras et al., 2019; Digby et al., 2013; Leach et al., 2016). Overall, PAM is well-suited for rapidly assessing the presence and habitat use of vocal species, as well as intraspecific changes in activity patterns and encounter rates over time, over large geographical areas. As such, PAM is a suitable method for detecting human-induced impacts and for assessing the success of conservation strategies (Astaras et al. 2020; Kalan et al., 2015).

2. Population metrics

It is important to consider a priori which population metrics are desired and attainable (Stephenson, 2019). Is a one-off measure of population or community status sufficient, or is it necessary to monitor changes over space or time? Is it important to measure population density, or are encounter rates sufficient? Here we consider the costs and benefits of analytical methods for generating three types of data outputs (in ascending order of usefulness in terms of potential applications and information gain): 1) encounter rate, also referred to as relative abundance or trap rate; 2) occupancy, i.e. the proportion of sampled sites occupied; and 3) population density, the number of animals per unit area.

2.1 Encounter rate

The encounter rate, *i.e.* the number of detections per unit of effort, is the most basic metric of biodiversity, as it does not require any additional parameters. However, comparing encounter rates across sites or time should be done with caution as variable detection may cause serious bias (Sollmann et al., 2013; Strindberg & O'Brien 2012). Detectability of animals varies with the weather, vegetation, visibility due to the season, monitoring equipment, survey design, animal size and behavior, and numerous other factors (Bas et al., 2008; Buckland et al., 2001; Cusack et al., 2015; Kolowski & Forrester, 2017; Madsen et al., 2020; Moore & Kendall, 2004; Pollock et al., 2002). As a result, observed differences in encounter rates may simply reflect differences in detectability rather than differences in population sizes (Sollmann et al., 2013). Constant detection probability may be achieved *within* sites with strict monitoring protocols, but it is more problematic to achieve *across* sites. For this reason, metrics that account for variation in detection probability are necessary for comparisons across sites, seasons and species.

2.2 Occupancy

Occupancy refers to the proportion of sampled sites occupied by a species. Since MacKenzie's seminal paper on ways of accounting for imperfect detection in wildlife surveys (MacKenzie et al., 2002), occupancy modelling - now a broad family of models - has become a widely used analytical method in wildlife monitoring, especially for elusive species for which estimates of absolute abundance (section 2.3) are rarely possible due to low overall detections. Occupancy modelling improves naive estimates of occupancy – i.e., the proportion of sites where the species was observed – by correcting for the probability of a missed detection when the species is in fact present. This probability is estimated based on the detection history in the sites where the species' presence was confirmed, and requires multiple survey periods (replicates either in space or time). Occupancy estimates based on occupancy modelling can be used

Table 1. An overview of how observations by humans, camera traps and passive acoustic sensors relate to the characteristics of interest for the four questions discussed in this paper. The field methods are rated high, medium or low, indicating a relative approximation of their suitability for each of the characteristics.

Questions	Characteristics	Observations by humans on line, point or recce transects	Camera trapping	Passive acoustic monitoring
1. Species coverage	Detection of ground-dwelling mammals and birds	Medium	High	Medium
	Detection of arboreal mammals and birds	Medium	Medium	High for vocal species
	Detection of amphibians	Medium	Low	High for vocal species
	Detection of reptiles	Medium	Low	Low
	Detection of insects	Medium	Low	High for vocal species
	Detection of bats	High with handheld bat detectors	Low	High
	Elusive, shy and rare species	Low	High	High for vocal species
	Suitability to assess whole communities	Low	High	High for vocal species, also through soundscapes
	Common biases for community assessments particular to the method	Timing of the survey; animal size; animals' avoidance of observers; observer skills	Installation location (*e.g.* close to the ground, on trails); animal size)	Uncertainties in estimating distance of detected animals and group size; ambient noise; calling frequency affected by behavioral and abundance changes
	Ways of maximizing observations when targeting specific species	Targeting trails or other often used habitat characteristics, BUT this cannot be used if assessing either density or encounter rate	Targeting trails or other often used habitat characteristics, using bait, BUT this cannot be used if assessing either density or encounter rate	Setting acoustic grids during specific seasons (e.g. breeding period for birds, when males will be calling)

Table 1 Continued

Questions	Characteristics	Observations by humans on line, point or recce transects	Camera trapping	Passive acoustic monitoring
2. Population metrics	Feasibility for counting detections (encounter rates)	High	High	High
	Feasibility for estimating occupancy	High	High	High
	Feasibility for estimating density	High for line and point transects, not possible for recces	Medium to high	Low
	Analytical methods for density estimations	-Distance sampling	-Distance sampling -Capture recapture -Random encounter modelling	None that are widely available. Distance sampling and capture recapture are in the experimental stages of development
	Precision of density estimates	Medium to high	Medium to high	Low to Medium
	Reproducibility of the data	Low to medium	High	High
3. Species identification	Approaches for observations / data annotation	-Direct observations -Indirect observations (requires production and decay rates) - Some citizen science (e.g. for birds or butterflies)	-Manual -Automated -Citizen science	-Manual -Automated (unsupervised or species specific classifiers) -Citizen science
	Technical expertise required for data annotation	Low	Medium	High
	Potential for automation	Low	High	High
4. Resources required	Relative costs of monitoring equipment	Low	High	High
	Costs of software and hardware for species identification	Low	Medium	High when detection algorithms have to be developed; Medium when detection algorithms are available
	Costs of training for fieldwork	High	Medium	Low
	Costs of field labor	High	Medium to high	Medium to high
	Time required for species identification	Low	High when detection algorithms have to be developed; Medium when detection algorithms are available	High when detection algorithms have to be developed; Medium when detection algorithms are available
	Costs of logistics	High	Medium to High	Medium

to compare population trends across space and time, without the risk of patterns being confounded by variable detectability (section 2.1). A key advantage of modelling occupancy based on camera trap or PAM data is that no additional parameters are required, as opposed to density estimation (section 2.3). Another important class of occupancy modelling are bayesian approaches (Royle & Kéry, 2007), which allow for more complicated multispecies models, deriving additional metrics and incorporating prior information. Leading software for occupancy modelling includes PRESENCE (Hines, 2006) and the R-library "unmarked" (Fiske & Chandler, 2011).

The repeated observations of presence/absence that are necessary to estimate detectability in occupancy analysis, can be achieved in various ways. Observations collected by humans ideally require multiple field visits to each site (Kendall & White, 2009; Guillera-Arroita et al., 2010), but these visits must be sufficiently close in time to ensure that animal distribution does not change between visits. This additional effort may add substantial costs, particularly in more remote areas. Models exist that allow for obtaining spatial replicates with a single team and a single visit, e.g., by treating fixed-length sections of a long transect as separate survey periods (Hines et al. 2010, Guillera-Arroita et al., 2011). For camera traps and PAM surveys, repeated survey periods can be obtained by dividing a single deployment period in fixed-duration sub-periods, e.g. a month-long deployment split into six 5-day survey-periods. The duration of these sub-periods is decided based on the characteristics of the species monitored, and should be sufficiently long to assume that repeated detections in subsequent survey periods are independent of earlier detections. Generally, once a minimum-duration survey period has been decided on, additional longer survey periods can be considered to ensure that the detection probability per survey period is not too low, e.g., <20% per survey period (Gálvez et al., 2016; MacKenzie & Royle, 2005). It is commonly recommended to let the size of the sampling unit, defined by grid cell area or recording unit spacing, be greater than the largest home range size of the target species, to avoid the need to correct for spatial correlation across sites. This, however, is usually unfeasible for species with very large home ranges.

Although occupancy can be a viable alternative to population density (e.g., Beaudrot et al., 2016; Devarajan et al., 2020), studies exploring whether occupancy has a linear relationship with density estimates have shown mixed results. While some studies show that the relationship approaches linearity (Linden et al., 2017; Tempel & Gutiérrez, 2013), other studies indicate that occupancy does not reflect density when species are rare (Gaston et al., 1998). Occupancy modeling does not work well for rare species because detection and occupancy become harder to separate, this problem can be partly alleviated by modeling occupancy of multiple species in the same model (using Bayesian approaches). The relationship also tends to vary with spatial and temporal sampling scales (Latham et al., 2014; Steenweg et al., 2018), or when species exhibit altered patterns of space use due to disturbances (Parsons et al., 2017). Non-linearity between occupancy and density implies that for the same animal species, in the same habitat, over the same period of time, occupancy can sometimes align with density, or be slightly different to it, or show a completely opposite trend, and should therefore be treated with caution (Parsons et al., 2017).

2.3 Population density

The most informative metric of wildlife monitoring is population density, *i.e.* the number of animals per unit area, which if extended over the species range, can be used to calculate population size (also referred to as absolute or true abundance). Accurate density estimates are important for effective management of wildlife, as they can provide the most robust picture of population trends over space or time (Plumptre & Cox, 2006). These trends can be used to quantify responses to, for example, disturbance, management or invasive species, and to inform sustainable management of exploited species (van Vliet & Nasi, 2008). The international classification of species conservation status on the IUCN Red List of Threatened Species and subsequent conservation strategies often require not only an understanding of the direction and magnitude of population trends (which could theoretically be obtained using occupancy), but, at least for IUCN Categories C and D, also information on the absolute size of a species' population is needed (IUCN 2020). This section discusses the three leading analytical methods for estimating population density: distance sampling, the random encounter model, and capture recapture, although various other analytical methods exist (Gilbert et al., 2020).

Distance sampling

Distance sampling by human observers along line or point transects in tropical forests is a well-established analytical method for density estimation (Buckland et al., 2001), for which free software (Distance) is available (Thomas et al., 2010). To convert the number of observations (individual, group or sign) to density estimates, distance sampling estimates the effectively surveyed area by calculating the rate of decrease of species' detection probability, with distance from the observer. Distance sampling therefore requires accurate measurements of these distances. Camera trap data have also been successfully used as point transects (Bessone et al., 2020; Cappelle et al., 2019; 2020; Howe et al., 2017), which requires the recording of distances at which recorded animals pass in front of the camera. Numbers of replicates (points) and detections (distance measurements) required for robust estimation are comparable to those required on line and point transects by human observers (Bessone et al., 2020; Cappelle et al., 2020). Analytical advances in image recognition are expected to automate such measurements, which will greatly speed up the process of density estimation using camera traps (Glover-Kapfer et al., 2019). For PAM, the distance of a vocalization cannot be inferred from volume alone, as the volume is also influenced by the direction in which the vocalization is emitted, atmospheric conditions and the intensity of the call (Alldredge et al., 2007). Sufficiently dense ARU arrays can triangulate sound locations, but this is at the cost of the overall spatial coverage achieved with a given budget (Marques et al., 2013; Mennill et al., 2012; Wrege et al., 2017). A key requirement of distance sampling is that sampling units (lines or points) capture the heterogeneity of the area surveyed, which is typically ensured by systematic sampling design (Buckland et al., 2001; 2010; Thomas et al., 2010). Sampling designs required for density estimation and broad-spectrum community application are the same (section 1), making it possible to estimate densities for multiple species.

Random encounter model

The random encounter model (REM) estimates density from trap rates by correcting the latter for the daily distance travelled by animals and the area sampled by camera traps (Rowcliffe et al., 2008). Sampled area is estimated in the same way as in distance sampling (Rowcliffe et al., 2011), and sampling design requirements are also identical. REM can only be used for camera trap data because the size of the sampled area needs to be known. REM requires estimates of animal speed of movement and daily activity level, which in principle can be estimated from camera footage (Rowcliffe et al., 2016), but this adds complexity.

Capture recapture approaches

Capture recapture analyses, including spatially explicit capture recapture which is now the standard, are an effective analytical method for species that are individually recognizable (Amstrup et al., 2010; Efford, 2004; Borchers & Efford, 2008), and are supported by a variety of analysis software (e.g. Efford, 2009, 2020; Laake, 2013; McClintock, 2015). This analysis is based on detecting and identifying individuals from part of a population in one sample, and then redetecting a proportion of these individuals in subsequent population samples. This way, the chance for an individual to be redetected in multiple samples is calculated and population density can be derived (Amstrup et al., 2010). Individual recognition is generally not possible with direct observations of tropical forest wildlife. Capture recapture analysis is widely used in camera trapping of species in which individuals have unique visual characteristics such as fur patterns, for example leopards and tigers, but also elephants and great apes can be recognized individually (Arandjelovic et al., 2010; 2011; Després-Einspenner et al., 2017; Head et al., 2013; Kane et al., 2015; Karanth et al., 1995; Rich et al., 2014). The approach can also be used with PAM for species with individually unique vocalizations (Dawson & Efford, 2009). Individual identification of large amounts of material can be facilitated by pattern recognition software such as hotspotter and Wild-ID (Nipko et al. 2020).

3. Species identification

With the advent of autonomous recorders, an often-overlooked part of wildlife monitoring is the effort required for species identification.

3.1 Human observation

For observations collected directly by humans, species identification is an integral part of the fieldwork, immediately identifying species or signs, or measuring distances, on the spot. Data are then recorded in a standardized format and only minimal extra steps are required to prepare the data for analysis.

3.2 Camera trapping

Camera trap surveys can produce thousands to millions of observations. Annotation and management of such volumes can be challenging for monitoring projects (Glover-Kapfer et al., 2019), despite the availability of various platforms for data management (Young et al., 2018). Image annotation by automated classification is developing rapidly (Glover-Kapfer et al., 2019; Willi et al., 2019; Whytock et al., 2021) and is increasingly being integrated in data management platforms (Ahumada et al., 2020) and desktop apps (Falzon et al., 2020), requiring gradually less technical expertise and improving access for mainstream use (Aodha et al., 2014). Algorithms can annotate images with increasing accuracy to species or genus level, or filter out empty images (Wei et al., 2020), which can drastically reduce the workload (Norouzzadeh et al., 2018; Tabak et al., 2019). The user can define the confidence thresholds that are deemed acceptable. Lowering these thresholds increases the number of annotated species, but also the margin of error. Confidence levels therefore directly affect the amount of observations analyzed, and should be reported to enable comparison of the output of automated methods between studies.

There are however limitations to the automated identification of less common species (Tabak et al., 2019), as building a robust classifier requires large amounts of annotated photos. The more species, the more annotated photos are needed to realize sufficient discriminative power of the algorithm. Additionally, the dense vegetation of tropical forests contains highly variable background colors, shapes and light conditions, making it more difficult to distinguish species in photos as compared to open landscapes. Emerging methods are finding solutions to this problem (Beery et al., 2019, 2020). However, as some images are difficult to identify even for humans (Meek et al., 2013), it is unlikely that human effort can safely be removed for rare species identification altogether in the foreseeable future.

3.3 Passive acoustic monitoring

For species detections with PAM, it is important to decide early on in a project how vocalizations will be detected in the recordings. This can be done manually by reviewing the spectrogram of the files both visually and acoustically (Aide et al., 2013; Bas et al., 2017; Knight et al., 2017; Ovaskainen et al., 2018). However, with multiple ARUs recording many hours of data each day, manual review quickly becomes impractical, making the use of automated classifiers desirable. These classifiers are not yet available for most species in tropical forests. Exceptions include elephants (Wrege et al., 2017), some primates (Heinicke et al., 2015; Zwerts et al., 2021) and birds (Priyadarshani et al., 2018). They do exist for gunshots, which can be used for eco-surveillance purposes (Astaras et al., 2017). Regardless of their availability, generally, the technical expertise required for using species-specific classifiers is moderately high.

Software facilitating the construction of new classifiers (Knight et al., 2017; Ovaskainen et al., 2018) includes a free web-based acoustic analysis platform (RFCx Arbimon; arbimon.rfcx.org). Robust classifier development often require a large annotated dataset (e.g. Enari et al., 2019; Gibb et al., 2019), which can be acquired either by manual annotation, or by the use of unsupervised classification which divides repeating patterns (vocalizations) into separate classes (Ovaskainen et al., 2018; Stowell & Plumbley, 2014). The output from this classification needs to be annotated. Existing databases (*e.g.* www.xeno-canto.org, www.macaulaylibrary.org) can be used to cross-reference vocalizations for most bird species (Araya-Salas & Smith-Vidaurre, 2017). For species that are not yet in these databases, expert knowledge is needed to annotate recordings. Unsupervised classification works well for regularly occurring vocalizations, but less so for rare species or rare vocalizations, as vocalizations will have a lower chance of detection or high risk of being masked by other sounds.

The annotations that are thus acquired, can be used to train species-specific classifiers. These can be sensitive to intra-specific call variations (Enari et al., 2019) and background noise (Knight et al., 2017; Priyadarshani et al., 2018), and have therefore shown mixed results when compared to manual classifications, both in terms of efficiency and accuracy (Brauer et al., 2016, Joshi et al., 2017; Blumstein et al., 2011). Furthermore, outcomes vary across classification methods, type of ARU, and species (Heinicke et al., 2015). Performance evaluation through manual cross-checking (Stowell et al., 2019) and rigorous reporting of analytical methods is therefore essential to safeguard the reproducibility of the data and to avoid false inferences (Digby et al., 2013; Kalan et al., 2015), as discussed for camera traps. In conclusion, most classifiers at the moment should be considered as semi-automated, as time-consuming human validation of the results is required.

Camera trap photos or acoustic data can also be annotated with the help of citizen science (Arandjelovic et al., 2016; Baker, 2016; Swanson et al., 2015). An example of that is Zooniverse, a citizen science platform driving identification of millions of camera trap images in many projects around the world (Simpson et al., 2014), and which is also increasingly being applied in combination with automated methods (Willi et al., 2019). Although citizen science can provide valuable input and can have wider benefits in terms of education and involvement, it can be time consuming to initiate and manage. Moreover, it may be of less use when species are not widely known or are difficult to identify.

4. Resources required

Each method comes with costs and it is important to plan realistically according to the available budget and staff capacity. Because of international price differences, we do not discuss absolute costs here, but rather indicate the relative importance of cost components of materials, labor and logistics specific to each method. For the sake of comparability, we focus on larger monitoring projects that cover extensive survey areas, requiring multi-day field missions. For absolute cost comparisons between the field methods, we refer to other literature (camera traps: Cappelle et al., 2019; Güthlin et al., 2014; PAM: Darras et al., 2019). Also not discussed here but very important to consider, is how many transects, camera traps and ARUs are necessary to provide acceptable confidence of estimates. Pilot studies may help in estimating how many sites should be surveyed and for how long, to get the best return on investment.

4.1 Human observation

Field observations require small initial investments for the monitoring or data processing equipment. Specific equipment purchases include a thread-based distance measurer, measuring tapes and binoculars. Standardized data recording is ideally done using a rugged device with the relevant software and recording structure installed (e.g. Spatial Monitoring and Recording Tool; smartconservationtools.org). The highest costs of human observations are related to salaries and fuel, due to an extensive training phase and continued time investment of field personnel. Thorough training is essential for multiple observers to standardize and develop the required skills base, including detailed taxonomic knowledge (Fitzpatrick et al., 2009). Typical courses for university-level field technicians last for about six to nine weeks, and regular refresher courses must be run to ensure standardization of methods across time and space (Maisels et al., 2008). Team sizes vary (but can be up to 14 people) depending on remoteness, on whether multiple specialized observers for various taxa are present, and the monitoring protocol.

Recces are roughly four times less costly than line/point transects (section 1.1) (Walsh and White 1999). If density is not required, occupancy models can be applied to recce data although one needs to be sure that enough effort has been planned to allow replication. If density is required, systematically designed line or point transects must be used, although a recce-transect combination increases the chance to detect less frequently occurring signs of wildlife or poaching. The length of line transects that can be covered in a day in tropical forests (an approximate 1-4 km) depends on forest type, wildlife density and terrain characteristics. Teams sometimes spend weeks at a time in the forest, either to take repeated observations for occupancy estimations, or to cover extended areas (Cappelle et al., 2019; Diggins et al., 2016). Monitoring large areas can thus weigh heavily on costs of labor, rations and field equipment.

4.2 Camera trapping

The initial investment for camera traps is relatively high, ranging from 150 to 800 USD per camera trap for midrange to high-end models. Apart from the device itself, SD cards, batteries, locks, hard disks and sometimes security boxes are required. Due to high humidity and termites in tropical forests, a percentage of camera traps can fail. In addition, cameras may get damaged or be stolen, so extra cameras should be purchased as backup (Glover-Kapfer et al., 2019; Meek et al., 2019). During camera trap installation and recovery missions, around 10 to 15 km per day can be covered. The field teams are generally made up of two to five persons, but may be larger depending on the survey area and the number of cameras. One to two persons per team require in depth training in camera trap installation, as the orientation of the cameras, and assuring random/ systematic location requires an understanding of the errors engendered by poor field practice (Roberts, 2011). Batteries may last for several months. Thus, installation, maintenance and recovery missions do not have to be scheduled frequently, resulting in relatively low logistical costs. However, regularly relocating camera traps improves the precision of estimates more than monitoring at the same locations longer (Fewster et al., 2009, Kays et al. 2020), lowering initial investments into materials but increasing salary costs. For camera traps, the workload shifts from fieldwork to image processing (section 3.2), with associated costs for employees that have received at least moderate levels of training in the use of database software and species identification.

4.3 Passive acoustic monitoring

Initial investment for PAM is generally high, as an ARU costs in the range of 250 - 600 USD (Darras et al., 2019), although low cost (<200 USD) alternatives exist (Hill et al., 2018). Costs of batteries and SD cards and the size of field teams (two to five persons) are comparable to those of camera traps. As sound recordings quickly result in sizable datasets, much larger than with camera trap images, data storage can be costly. Unlike camera traps, relatively little training is required to set up ARUs, as the installation location is less likely to introduce biases in data collection. While ARUs can record continuously for several days or weeks, depending on the target species, they can be programmed to record according to a predetermined schedule (e.g. only during morning chorus) and for a limited frequency range (thus reducing the size of files generated per recording session), thereby extending the overall deployment duration with a set number of batteries and as such decreasing operational costs. As with camera traps, the limited spatial replication can be compensated by regularly relocating the ARUs, which in turn inflates fieldwork and logistical costs. For PAM, the workload also shifts from fieldwork to data processing, and even more so than with camera traps, PAM requires highly trained technicians (section 3.3). Data processing also involves fairly high computing power, requiring investment for either a modern multi-core computer or cloud computing services. Web-based platforms require access to high speed internet connection to upload the typically very large acoustic files.

5. Concluding remarks

Given the intricacies of each method and the widely varying objectives and circumstances of wildlife monitoring efforts, it is not possible to make universally relevant prescriptions for action stemming from this review. The relative advantages of each monitoring method are always context dependent and the result of a complex web of equally important details. Guidance as to which field method is most adequate in any particular situation can be found by answering the four key questions we posed in this review. The answers to question 1 and 2 should match the monitoring objectives, as each method allows the detection of some species but not all, which should be taken into account when doing community studies. The answers to questions 3 and 4 depend on the available budget, time and skills. Monitoring is most effective if the objectives are clearly defined (Stephenson, 2019; Yoccoz et al., 2001). Decision trees (e.g. Hedges et al., 2012; Kühl et al., 2008; Strindberg & O'Brien, 2012) can help to define these objectives. Central to any monitoring objective is whether a project targets either a specific species or the entire community, as well as which population metric is required. Aside from setting objectives, it is necessary to acknowledge the realities in the field with regard to the availability of financial and human resources for fieldwork and data processing, and select field methods accordingly. Not fully considering the trade-offs between achieving the objectives and the attainability of a survey in relation to a particular method, may ultimately lead to ineffective monitoring and loss of conservation funds (Nichols & Williams, 2006; Sheil, 2001).

Despite current bottlenecks associated with camera trapping and PAM, the technological landscape is quickly evolving. Many people and organizations are working hard to improve efficiency both in data collection and processing through the development of new platforms and tools (e.g. RFCx Arbimon, Zooniverse, Wildlife Insights (Ahumada et al., 2020; Simpson et al., 2014)). Moreover, apart from the methods discussed here, exciting new genetic methods with much promise to monitor terrestrial and aquatic species, also merit attention. They can provide information on species diversity within a community (using e-DNA), animal density (using spatially explicit capture-recapture techniques), individually known animals (if one wants to assess the entire population in a small area), sex ratios and taxonomy (Bohmann et al., 2014).

Integrated monitoring using multiple methods are, despite complementary strengths, rarely combined (Buxton et al., 2018; Garland et al., 2020), mainly due to the costs involved, but also due to a lack of cross-methodological knowledge exchange. Of course, any one method requires significant technical know-how and financial resources, which are not always readily available. Yet, we encourage combining field methods, as it has the potential to greatly broaden the diversity of species monitored. In addition, using multiple methods may facilitate synergies for more in-depth ecological or behavioural research (Garland et al., 2020; Moore et al., 2020), opening up new, interdisciplinary, research paths that can ultimately help to answer pressing ecological questions and provide improved guidance for conservation policy.

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Trees make a forest, but a forest is not only made up out of trees.

Chapter 3

FSC-certified forestry benefits large mammals compared to non-FSC

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This chapter is, at the time of writing this thesis, under review for publication by the journal Nature.

Abstract

The majority of tropical forests are exploited for timber (Blaser et al., 2011). This has extensive impacts on biodiversity and ecosystems, primarily through the creation of roads which facilitates hunting for wildlife over extensive areas. Forestry certification systems such as the Forest Stewardship Council (FSC) are expected to ameliorate impacts on biodiversity but to date very little is known about the effectiveness of FSC certification due to research design challenges (Romero et al., 2018; van der Ven & Cashore, 2018). Here we provide this evidence by using 1.3 million camera trap photos of 55 mammal species in 14 logging concessions in Western Equatorial Africa. We observed more wildlife in FSC-certified than in non-FSC logging concessions. The effect was most pronounced for species weighing over 10 kg, and for species of high conservation priority such as the Critically Endangered forest elephant, large carnivores and primates. Across the whole wildlife community, non-FSC concessions contain proportionally more rodents and other small species than FSC-certified concessions. Our findings provide consumers, governments, and NGOs with convincing data that FSC-certified forestry is less damaging to the mammal community than non-FSC forestry. This study provides strong evidence that FSC-certified forest management, or equivalently stringent regulations and controlling mechanisms, should become the norm for timber extraction, since inaction will result in half-empty forests dominated by rodents and other small species.

Introduction

Commercial timber concessions cover over one-quarter of the world's remaining tropical forests (Blaser et al., 2011). Forest certification systems like the Forest Stewardship Council (FSC) aim to have more positive socio-economic and environmental outcomes compared to conventional logging schemes. A positive influence of FSC certification has been demonstrated in relation to reduced deforestation (Tritsch et al., 2020), and for social aspects, such as working and living conditions of employees and benefit sharing with neighbouring institutions (Cerutti et al., 2014). Previous studies also suggest that mammal occupancy in FSC-certified sites is comparable to that of protected areas (Roopsind et al., 2017; Tobler et al., 2018). Yet, little is known about the impact of FSC certification on wildlife compared to non-FSC forestry (Romero et al., 2018; van der Ven & Cashore, 2018).

A major concern for biodiversity is that timber extraction – by the creation of roads – creates access to previously remote forests, which facilitates illegal and unsustainable hunting (Benítez-López et al., 2017; Kleinschroth et al., 2019; Laurance et al., 2009). FSC certification may diminish these negative impacts because, among other measures, companies have to reduce accessibility to concessions by closing off old logging roads, prohibit bushmeat transport or hunting materials and have surveillance by eco-guards. Logging companies are third party audited for compliance on a yearly basis (Connie J Clark & Poulsen, 2012) (Tables S1 & S2). Most previous studies on the effectiveness of FSC certification concerning wildlife conservation have focused on one or a few sites or species at a time (Bahaa-el-din et al., 2016; Polisar et al., 2017; Sollmann et al., 2017; Stokes et al., 2010). Although these studies reported a positive impact of FSC certification on wildlife compared to non-FSC concessions, their research designs did not account for explanatory variables like concession location, land-use history or stochastic effects (Burivalova et al., 2017; Ramage et al., 2013). To our knowledge, only one study included multiple sites and species and found no effect of FSC certification. However, that study investigated bird diversity, which is not an abundance metric (Campos-Cerqueira et al., 2019). Quantifying changes in populations is important because hunting not necessarily completely extirpates wildlife species, especially when forests are connected, but rather results in population declines (Benítez-López et al., 2017).

Here we used camera traps to assess whether FSC certification can mitigate the negative effects of timber extraction by studying the encounter rate of a broad range of species across multiple sites. We compared mammal observations across seven paired FSC-certified and non-FSC concessions in Gabon and the Republic of Congo (Fig. 1). Western Equatorial Africa (WEA) is particularly suitable for these analyses, as its forests are reasonably intact and therefore its logging concessions are mostly devoid of influences other than the effects of logging itself (Grantham et al., 2020; Plumptre et al., 2021; Potapov et al., 2017). In this region, most forestry concessions are embedded in a matrix of contiguous forest, and bushmeat hunting is pervasive. Logging increases hunting pressure by increased access (logging roads) and by the arrival of people working in the concessions in once-remote forests (Abernethy et al., 2013; J. R. Poulsen et al., 2011; Ripple et al., 2016). We included all but one of the FSC-certified companies in WEA. Local pairing of FSC-certified and non-FSC concession types reduces the influence of regional landscape heterogeneity. We calculated mammal encounter rate to assess the impact of FSC-certified logging and used the presence of hunting signs around each camera to estimate hunting pressure. We then grouped mammal species into five weight classes, as the relative encounter rate of these classes can also be used as a proxy for hunting pressure. This is because larger bodied species are targeted more by hunters (Abernethy et al., 2013; Wilkie et al., 2011), and recover more slowly from hunting compared to smaller bodied species, resulting in lower abundances of large versus small species under higher hunting pressure (Atwood et al., 2020; Cardillo et al., 2005). Finally, we explored how FSC-certified forestry affects mammal encounter rate by taxonomic group and by IUCN Red List categories (IUCN, 2022). We hypothesized that FSC certification effectively decreases hunting pressure and predicted a higher encounter rate of larger-bodied species in FSC-certified than in non-FSC logging concessions.

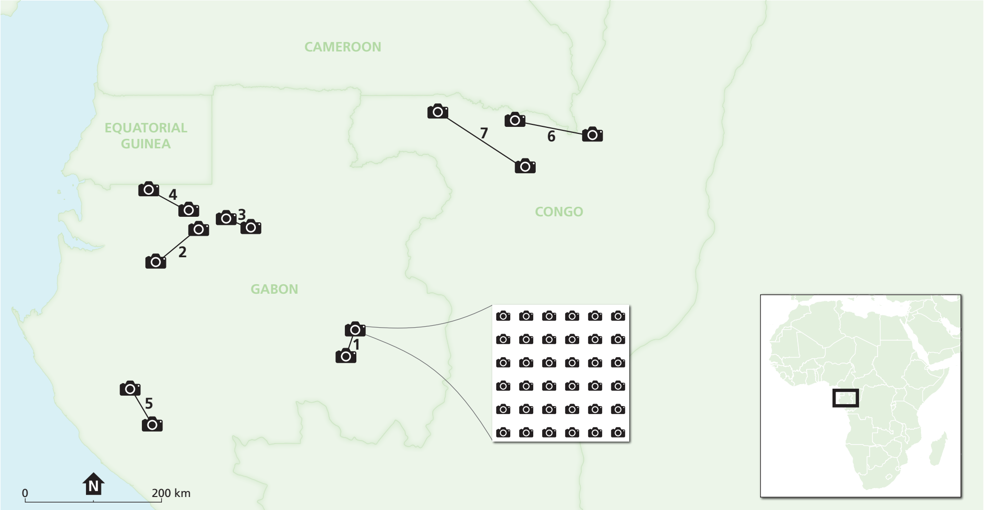

Figure 1. Locations of the 14 study sites in Gabon and the Republic of Congo. Numbers and lines indicate the pairs of concessions.

Results

We collected and labelled nearly 1.3 million photos from 474 camera traps with a total effort of 35,546 days, averaging 2,539 camera trap days per concession (Table S3). We detected 55 mammal species and found a 43% higher overall mammal encounter rate (Fig. 2A) and fewer signs of hunting (Fig. 2B) in FSC-certified compared to non-FSC concessions (Tables S4 & S5). We did not find marked differences in overall species diversity between the two concession types.

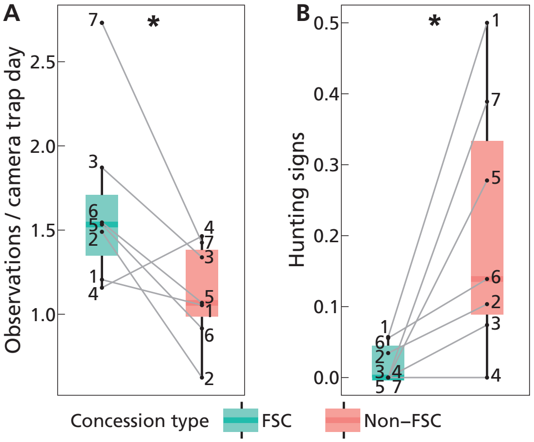

Figure 2. Wildlife and hunting observations in FSC-certified and non-FSC concessions. (A) Encounter rate of all observed mammals, and (B) proportion of camera locations with hunting signs. Numbers in the plot represent the seven pairs of FSC-certified and non-FSC concessions linked by grey lines. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank, *: $p < 0.05$.

The relative differences between mammal encounter rates in FSC-certified and non-FSC concessions increased with body weight (Figs. 3A & Fig. S1; Table S5). FSC-certified concessions had a higher encounter rate of mammals above 10 kg than non-FSC concessions, but there was no difference for mammals below 10 kg. Mammals in weight classes >10 kg were 1.8 to 4 times more frequently observed in FSC-certified concessions than in non-FSC concessions. Mammal encounter rate in FSC-certified and non-FSC concessions varied across IUCN Red List categories (Fig. 3B; Table S5). In particular, the encounter rate of Critically Endangered mammals was four times as high in FSC-certified as in non-FSC concessions.

Mammal encounter rate in FSC-certified and non-FSC concessions varied between taxonomic groups (Fig. 4; Table S5). Forest elephants were observed 4.7 times, pri-

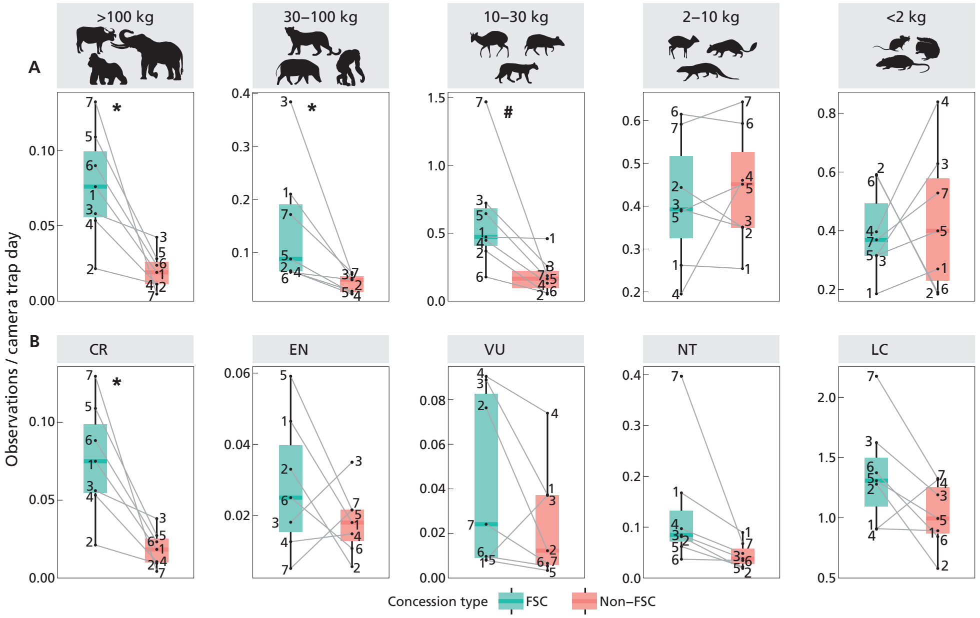

Figure 3. Mammal encounter rate across weight classes and IUCN Red List Categories in paired FSC-certified and non-FSC concessions. (A) Five weight classes, and (B) five IUCN Red List categories. IUCN abbreviations: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern. Numbers in the plot represent the seven pairs of FSC-certified and non-FSC concessions linked by grey lines. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank, *: $p < 0.05$, #: $p < 0.1$. Note that the scales of the y-axes vary. See Methods for symbol credits and licensing.

mates 2.4 times and even-toed ungulates 1.5 times as frequently in FSC-certified as in non-FSC concessions. The encounter rate of other taxonomic groups did not differ.

When differentiating between large and small species within taxonomic groups, the encounter rate of large carnivores was higher in FSC-certified than non-FSC concessions (Fig. S2; Table S5). Forest antelopes displayed a similar pattern: the large yellow-backed duiker and the medium-sized red duikers were observed more frequently in FSC-certified concessions, whilst the small blue duikers did not differ in encounter rate. Great apes and monkeys were more abundant in FSC-certified than non-FSC concessions, although the difference was not significant. The encounter rates of pangolins did not differ significantly.

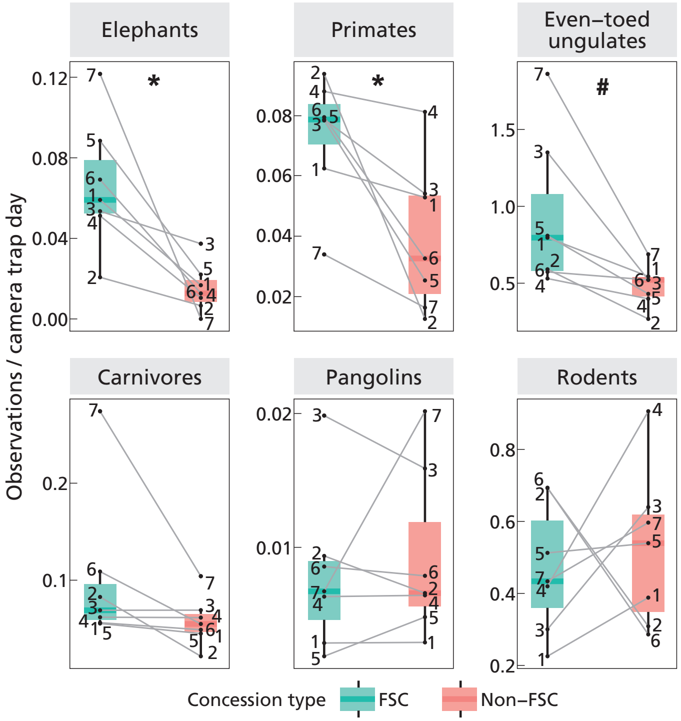

Figure 4. Mammal encounter rate across six taxonomic groups in paired FSC-certified and non-FSC concessions. Numbers in the plot represent paired FSC-certified and non-FSC concessions linked by grey lines. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank, *: $p < 0.05$, #: $p < 0.1$. Note that the scales of the y-axes vary. See Methods for symbol credits and licensing.Estimated total faunal biomass derived from mammal encounter rates was a factor 4.5 higher in FSC-certified compared to non-FSC concessions. Larger species contributed more to the total biomass (Figs. S3 & S4). Estimated total biomass per country shows similar patterns (Fig. S3).

Discussion

The loss of large wildlife

This study is, to our knowledge, the first large-scale quantitative study assessing the impact of FSC-certified forestry on mammal encounter rate across multiple logging concessions and for a broad range of mammals. Our data provide strong evidence that FSC-certified forestry results in higher overall mammal abundance as approximated by encounter rate and faunal biomass relative to non-FSC forestry. This effect was most pronounced for Critically Endangered species, and for species larger than 10 kg, which was consistent for all FSC-non-FSC concession pairs, likely because the latter recover more slowly from population losses and may be targeted more by hunters (Atwood et al., 2020; Ripple et al., 2014). Forest elephants, primates, large carnivores and medium to large forest antelopes were all encountered more frequently in

FSC-certified concessions. Not all large species with reduced encounter rates may be commonly targeted for hunting, but they are often indiscriminately affected by snaring (Figel et al., 2021). Non-FSC concessions contained proportionally more rodents and other small species than FSC-certified concessions (Table S4). Potential hunting pressure on their populations might be compensated by higher reproductive rates, or a release from competition and predation in the non-FSC concessions (Yasuoka et al., 2015; Young et al., 2016).

A particularly strong effect of FSC certification was found for the Critically Endangered forest elephant, which is in line with previous findings (Stokes et al., 2010). The distribution of this species is driven almost entirely by human activity as they avoid areas that are unsafe to them (Maisels et al., 2013; Wall et al., 2021). Considering their large home ranges that can span multiple concessions (Beirne et al., 2021), they may actively seek to reside not only within protected areas, but also in FSC-certified concessions where measures to prevent illegal hunting are in place. This suggests that FSC-certified concessions may provide an important refuge for wide-ranging elephants. In contrast, no difference was found in pangolin encounter rate between the two types of logging regimes. All three pangolin species had low encounter rates (Table S4), which reduces our ability to draw strong conclusions about these species. Pangolins are among the most trafficked mammals which warrants further research (Challender et al., 2020).

We detected no differences in overall species diversity, nor did we expect to. This is because human population density in the main forest blocks in Western Equatorial Africa is relatively low, and the forests still have high connectivity over much of their area.

Conservation of large mammals through FSC certification brings wider benefits to forests, since the affected mammals play a pivotal role in these ecosystems. Loss of wildlife results in modification of the vegetation structure and alterations in delicate ecological processes such as seed dispersal, seed predation, browsing, plant competition, nutrient cycling and predator-prey interaction (Rogers et al., 2021). Moreover, large mammal abundance has been reported to be positively correlated to forest carbon storage (Bello et al., 2015; Berzaghi et al., 2019; Chanthorn et al., 2019; Peres et al., 2016; John R. Poulsen et al., 2013), and the benefits of their conservation may far outweigh the cost (Berzaghi et al., 2022). In addition, by being more biodiverse and providing less bushmeat for the markets, FSC-certified concessions or similar stringent schemes may also reduce the chance of zoonotic disease transmission (Johnson et al., 2020; Olival et al., 2017).

Methodological considerations

For the sections of the concessions that we sampled, we ensured comparability between concessions by maximizing similarity in geographic factors that may drive variation in wildlife abundance: elevation and distances to roads, rivers, human settlements and protected areas between each pair of FSC-certified and non-FSC concessions (Fig. S5; Table S6). Precise logging intensity and logging history data per camera were not available for most concessions because the companies' planning schemes and actual exploitation of cutting blocks often did not match. Slight differences in logging history are not expected to have a large effect on the data, because wildlife is mobile and returns quickly to areas that have been exploited (Morgan et al., 2018). Altogether, the differences between FSC-certified and non-FSC concessions that may drive wildlife abundance, were non-significant. Lastly, fourteen forestry concessions may be a large sample size for tropical ecology studies (Ramage et al., 2013) but a low sample size from a statistical perspective. Nonetheless, despite the small number of replicates, we found clear and consistent differences in encounter rate between FSC-certified and non-FSC forests.

We used encounter rate, defined as the number of observations divided by the number of camera trap days, as our metric of abundance. Using encounter rates has the advantage that species can be grouped for comparisons (e.g. weight classes), as opposed to using an occupancy modelling approach. Encounter rates may be affected by unaccounted influences on detection probabilities, which may complicate comparisons between species, or between sites. We compare individual species across management types, which renders differences in detection across species irrelevant. For camera trap sites however, variation in visibility or other factors may affect the number of detections, even though wildlife populations sizes are similar. Yet, we did not find differences in any relevant site covariates at the camera trap level: visibility at ground level, slope, the presence of fruiting trees and small water courses around camera trap locations did not differ between FSC-certified and non-FSC concessions (Figs. S7 & 8; Table S6). We also compared the presence and type of trails or paths around camera trap locations, which did not differ significantly except for the number of elephant paths, which was higher in FSC-certified concessions (Fig. S6; Table S6). As camera traps were installed randomly on the nearest tree with four metres visibility to the predetermined GPS locations, finding a higher frequency of elephant paths in FSC-certified concessions was, in itself, an indication of higher elephant abundance in FSC-certified concessions. Lastly, potential seasonal influences are accounted for by the paired design.

Conservation implications

Of Central African tropical forests, 21.1% is designated for conservation (Doumenge et al., 2021), but 51% of the combined species range of western lowland gorillas and central chimpanzees and a large part of the species range of forest elephants, lie in logging concessions (Maisels et al., 2013; Strindberg et al., 2018). Protected areas are essential for conservation, but sometimes lack the resources for effective control of illegal hunting (Laurance et al., 2012; John R. Poulsen et al., 2017). However, forestry companies often do have the means to protect forests and have an economic incentive to do so. Our results confirm that FSC-certified forests substantially benefit larger and threatened species compared to non-FSC concessions. Well-managed logging concessions can help mitigate the negative effects of the forestry sector on biodiversity and contribute to Sustainable Development Goals 12 (Sustainable Consumption and Production) and 15 (Life on Land) by performing a strategic function in preserving habitats and landscape connectivity while allowing for responsible economic activity (C. J. Clark et al., 2009; Edwards et al., 2014; Ward et al., 2020). Non-FSC companies may also contribute to conservation, as they vary along a gradient of environmental and social responsibility (Rayden & Essono, 2010). This however was not the focus of our study.

Our findings indicate that FSC effectively controls the widespread and unsustainable hunting and poaching that is facilitated by the increased access to forests engendered by timber extraction. However, not all hunting is illegal, and FSC certification protects customary rights to hunt non-protected species for subsistence. Sustainability of this practice is controlled by - among other regulations - controlling firearm permits and monitoring wildlife offtake. We believe that a strict set of regulations, control of compliance and regular enforcement are all crucial for successful environmental protection through forest certification.

The necessity to upscale certification

We present a clear, evidence-based message about the positive impact of FSC certification and its efficacy as a conservation tool. We show that large and Critically Endangered mammals– that play vital functions in forests – are more abundant in FSC-certified concessions than in non-FSC concessions. This study calls for action, reinforcing previous studies that called for more forest certification and land-use planning that takes conservation into account (Maisels et al., 2013; Nasi et al., 2012; Stokes et al., 2010; Strindberg et al., 2018). To protect large wildlife, we urge that FSC certification or similar stringent schemes become the norm, as conventional logging is likely to result in half-empty forests dominated by rodents and other small species. To increase forestry companies' interest in FSC certification, it is essential that sufficient demand is created for FSC-certified products by institutional and individual buyers. The information put forward by this study can play an important role in FSC's global strategy to leverage sustainable finance to reduce biodiversity loss, whereby certificate holders can be rewarded for the biodiversity benefits that they incur (Forest Stewardship Council, 2020). Rendering FSC-certified forests eligible for payments by biodiversity schemes, especially driven by government regulation(Salzman et al., 2018), can contribute to fair valuation of standing forests. To ensure environmentally and socially responsible forestry (Cerutti et al., 2014), we strongly support application of regulatory frameworks that stimulate and require the selling and buying of timber certified by FSC or similar stringent schemes.

Acknowledgements

We thank the forestry companies for access to their concessions, 263 local recruits for fieldwork assistance and 23 students and assistants for data processing. The work was carried out with permission from the Gabonese Centre National de la Recherche Scientifique et Technologique (CENAREST) under research permit n°AV AR0046/18, and the Congolese Institut National de Recherche Forestière under research permit n°219 and n°126 issued by the National Forest Research Institute (IRF) of Congo with the help of the Wildlife Conservation Society (WCS) Congo, under number 219MRSIT / IRF / DG / DS on July 17, 2019 and the extension under number 126MRSIT / IRF / DG / DS e August 4, 2020.

Methods

Data collection

We set up arrays of camera traps from 2018 to 2021 in 14 logging concessions owned by 11 different companies (5 FSC and 6 non-FSC) in Gabon and the Republic of Congo (Fig. 1). Seven FSC-certified concessions were each paired to the closest non-FSC concession that was similar in terms of terrain and forest type (Grantham et al., 2020). All concessions are situated in a matrix of connected forests. Within each pair of concessions, camera traps (Bushnell Trophy Cam HD for pairs 1 - 6 and Browning 2018 Spec Ops Advantage for pair 7) were deployed simultaneously to account for seasonal differences, for two to three months. There was one exception where Covid restrictions obliged the cameras to remain in place for longer (Table S3). Camera trap locations within each pair of concessions were chosen based on similarity between potential drivers of animal abundance, including distance to settlements, roads, rivers, protected areas, elevation (Fig. S5; Table S6) and time since logging (2-10 years before our study), although some camera grids overlapped older logging blocks. Camera traps were set out in systematic, one-kilometre spaced grids with a random start point. Upon reaching the predetermined GPS locations, the first potential installation location was used where cameras had at least 4 metres of visibility. This ensured that each grid was representative of environmental heterogeneity: i.e. not specifically targeting nor ignoring trails or other landscape elements that could influence detection (Zwerts et al., 2021). The one-kilometre inter-camera distance exceeds most species' home range sizes to avoid spatial autocorrelation. Neither were species expected to emigrate within the sampling duration of the study. Between 28 to 36 cameras were deployed in each concession. Cameras were installed at a height of 30 cm to enable observations of wildlife of all sizes while ensuring that each camera had at least four metres visibility in front of it. Cameras were programmed to take bursts of three photos to maximize the chance of detection and to take a photo every 12 hours for correct calculation of active days in the event of a defect before the end of the deployment period. For each camera, we recorded whether there was an elephant path skidder trail, small animal trail, or none of the above within each camera's field of view (Fig. S6; Table S6). We also recorded forest visibility (0-10m / 11-20m / >20m), slope (0-5° / 5-20° / >20°), presence of fruiting trees within 30 m and presence of small water courses within 50 m (Figs. S7 & S8; Table S6). When approaching each predefined camera point, we recorded the presence of cartridges, snares and hunting camps from 500 m before the camera up to its location. Various field teams were employed in different sites and hence there may be some influence interobserver bias of hunting observations between sites.

Photo processing and data analysis

Camera trap efforts yielded 1,278,853 photos, including 645,165 photos with animals. All photos were annotated in the program Wild.ID, version 1.0.1. We identified animals up to the species level if photo quality permitted and otherwise designated the species as ‘indet’ (Kingdon, 2015). As reliable species identification of small mammals is difficult, they were grouped into squirrels, rats and mice and shrews. Rare observations of humans, birds, bats, reptiles and domestic dogs were excluded from the analyses.

Observations of the same species that were at least 10 minutes apart were considered as separate individuals of that species. We verified this threshold with a sensitivity analysis by calculating the number of observed individuals for 10, 30, 60 and 1440 minutes, which all yielded similar results. When multiple animals were observed, the number of individuals was determined by taking the highest number of individuals in a photo within the 10-minute threshold. Sampling effort was defined as the number of camera days minus down time due to malfunctioning cameras or obstruction of vision by vegetation.

Wildlife behaviour may be different in hunted concessions, as wildlife may be shyer for non-natural objects like camera traps, which would in turn negatively affect their probability of detection. If this dynamic indeed exists, this shyness was assumed to fade over time with habituation to the materials, resulting in an increase of observations over time. We tested for an interaction between certification status and the number of observations over time using a linear model with a log transformed number of observations for the first 65 days of all deployments, as that was the shortest concession deployment period, ensuring that all concessions were equally represented, but did not find that FSC certification affected a trend in observations over time (Fig. S9).

For each species for each concession, we calculated encounter rate as the number of observations divided by the sampling effort and we report all findings using the metric “Observations / day”. Encounter rate was calculated for all species combined, per weight class, per taxonomic group, per IUCN Red List category and within taxonomic groups for large versus small forest antelopes, carnivores, primates and pangolins (Table S7). Body weight of each species was determined by taking the mean across sexes (Kingdon, 2015). Taxonomic groups Hyracoidea and Tubulidentata were excluded from the taxonomic analysis due to low sample sizes. Shrews were included as rodents in the taxonomy analysis even though they are formally not, because they are difficult to distinguish from mice. We consider this acceptable given that shrews are functionally very similar to rodents in the light of this study. Lastly, to study the impact of certification on total estimated faunal biomass, the number of individuals of each species was multiplied by its average weight divided by the sampling effort. Biomass was also estimated separately for both study countries, to serve as a comprehensive analysis for exploring potential country specific effects.

Given the sample size of seven paired logging concessions, we used non-parametric tests for all analyses, applying two-sided Wilcoxon signed-rank tests for all binary comparisons. For the weight class, taxonomy and IUCN analyses, we calculated the relative difference in encounter rate between FSC-certified and non-FSC concessions by subtracting the non-FSC encounter rate from the FSC-certified encounter rate and then dividing this difference by the FSC-certified encounter rates. We then applied the Friedman test for the main effect. We used two-sided Wilcoxon signed-rank tests on the original data and report them without corrections in the main text and figures, as the loss of power and concomitant loss of statistical significance would decrease statistical clarity and reduce the ability to discern which groups are of relevance to the predicted, and observed, main effects (Dushoff et al., 2019). For completeness, we also report Holm corrected pairwise comparisons in Table S5. Statistical analyses were performed in RStudio version 3.4.1. Animal silhouettes added to figure 3 to visually represent a selection of mammals were either downloaded from PhyloPic (http://www.

phylopic.org) and available for use under the Public Domain Dedication license, or we created them ourselves.

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Supplementary materials

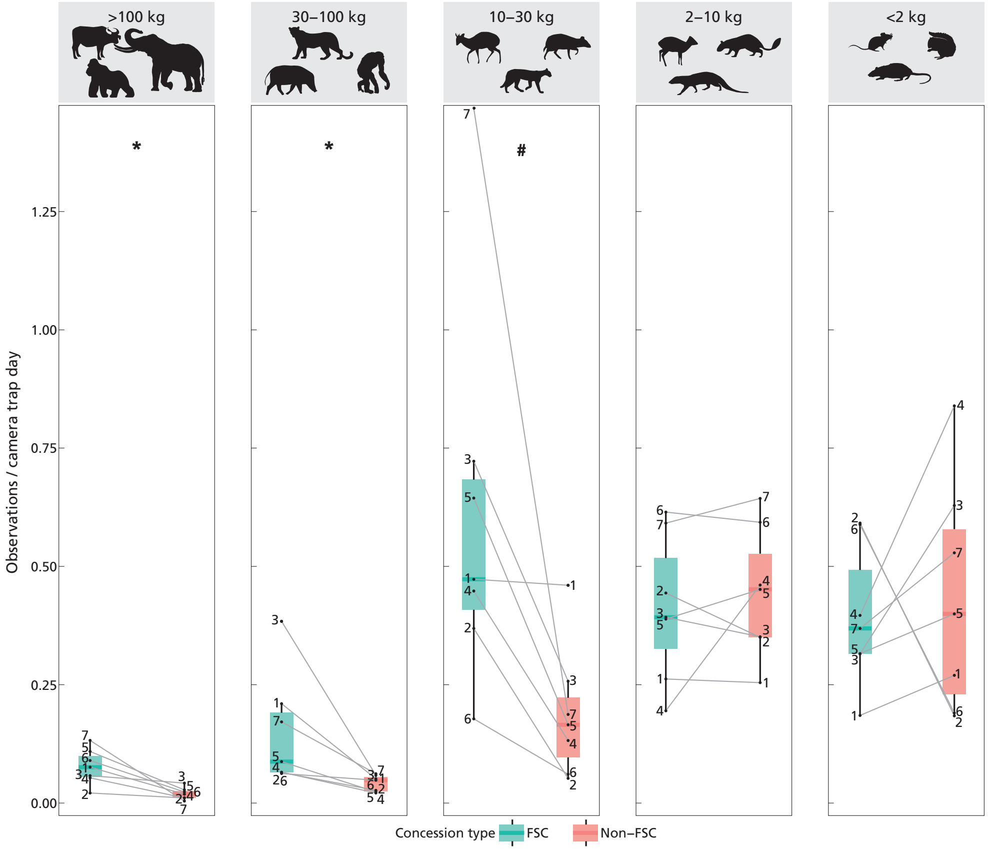


Figure S1. Mammal encounter rate across all weight classes in paired FSC-certified and non-FSC concessions. Mammals weighing more than 10 kg were observed more often in FSC-certified concessions than in non-FSC concessions. Y-axes are locked to facilitate comparisons of encounter rates across classes. Numbers in the plot represent paired FSC-certified and non-FSC concessions and are linked by grey lines. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank, *: $p < 0.05$, #: $p < 0.1$.

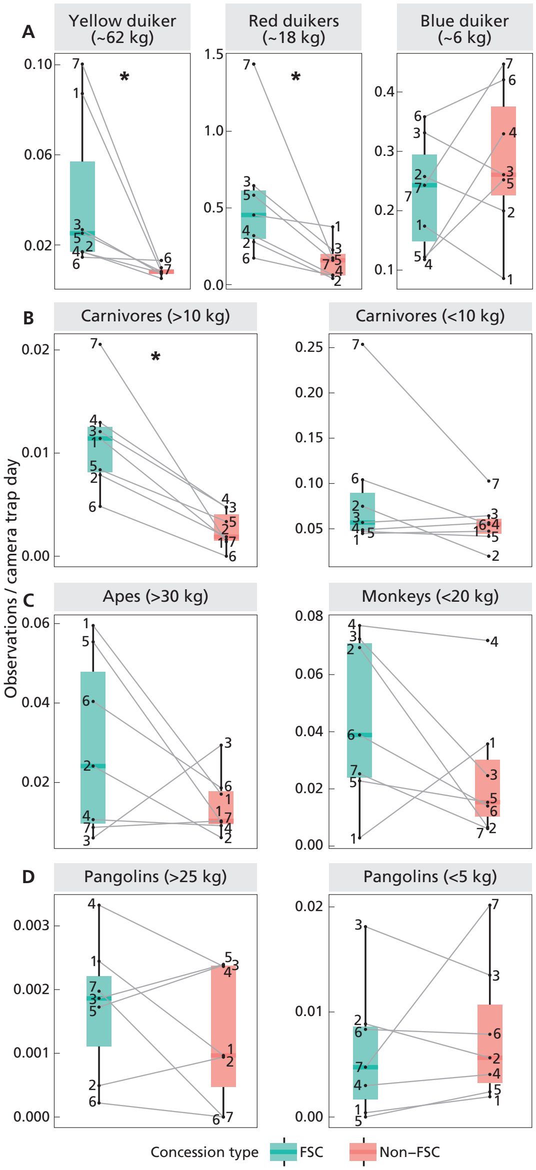


Figure S2. Mammal encounter rate of small versus large species within taxonomic groups in paired FSC-certified and non-FSC concessions. (A) Forest antelopes, (B) carnivores, (C) primates and (D) pangolins. Larger forest antelopes and large carnivores were both observed more frequently in FSC-certified concessions than in non-FSC concessions. No difference was found between management types for the great apes and monkeys, or large and small pangolins, although there was a much wider range of encounter rate estimates for both our categories of primate within FSC concessions. Pangolins were observed very infrequently in all sites, complicating the ability to detect potential differences between sites. Numbers in the plot represent paired FSC-certified and non-FSC concessions linked by grey lines. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank, *: $p < 0.05$, #: $p < 0.1$. Note that the scales of the y-axes vary.

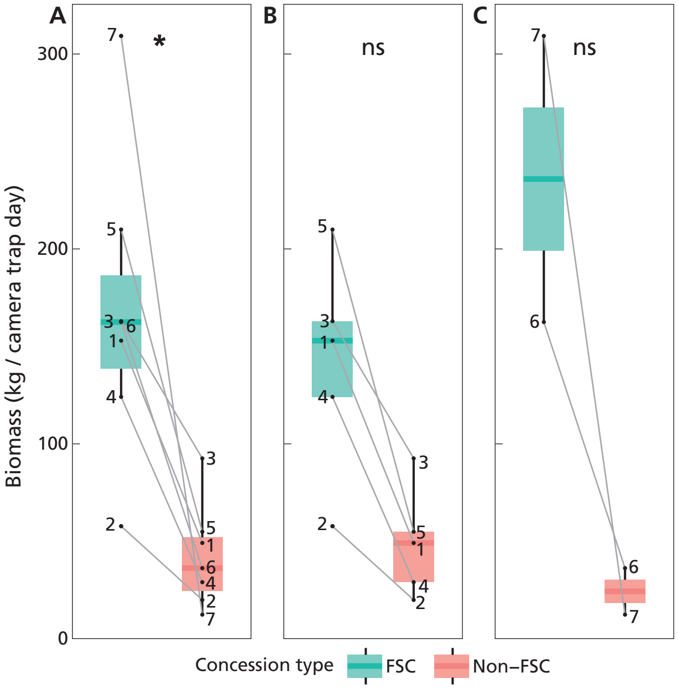


Figure S3. Estimated faunal biomass derived from mammal encounter rates was higher in FSC-certified than in non-FSC concessions. (A) All sites, (B) Gabon and (C) Republic of Congo. Numbers in the plot represent paired FSC-certified and non-FSC concessions linked by grey lines. Y-axes are locked. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank, *: $p < 0.05$.

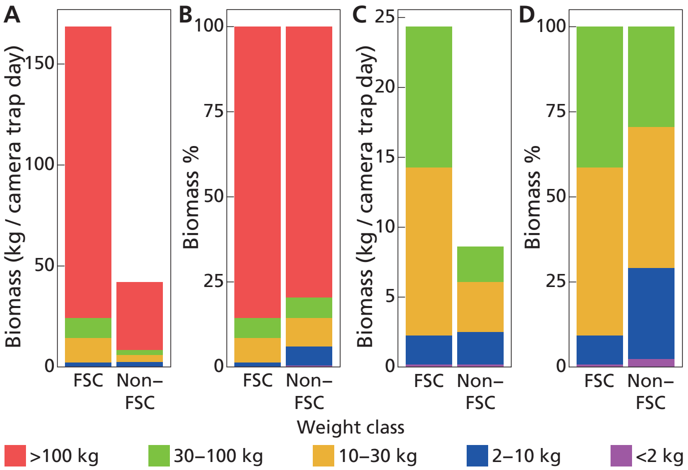


Figure S4. The contributions of different weight classes to the estimated faunal biomass derived from mammal encounter rates in FSC-certified and non-FSC concessions. (A) In kg / camera trap day; (B) as a proportion of total faunal biomass; (C) in kg /day for species up to 100 kg; (D) as a proportion of the total faunal biomass for species up to 100 kg. FSC-certified concessions had higher overall biomass whereby animals weighing more than 10 kg made up a larger proportion of the total biomass than in non-FSC concessions.

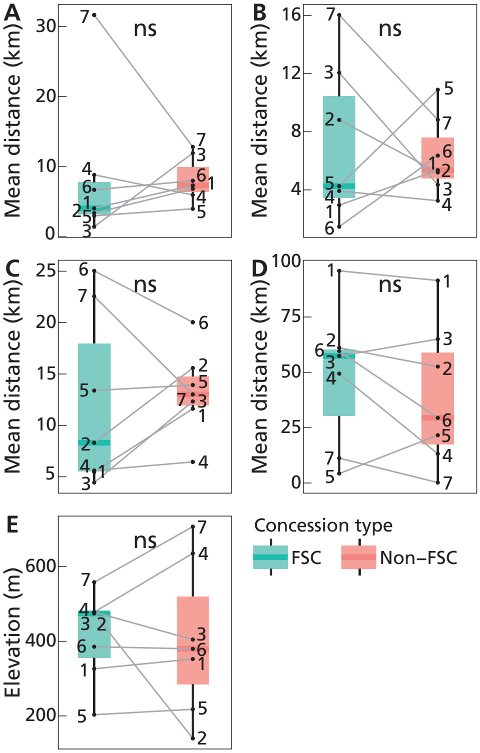


Figure S5. Distribution of all geographic covariates was similar for FSC-certified and non-FSC paired concessions. (A) Roads, (B) rivers, (C) human settlements, (D) protected areas and (E) elevation. Numbers in the plot represent paired FSC-certified and non-FSC concessions linked by grey lines. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank test, ns: $p > 0.05$.

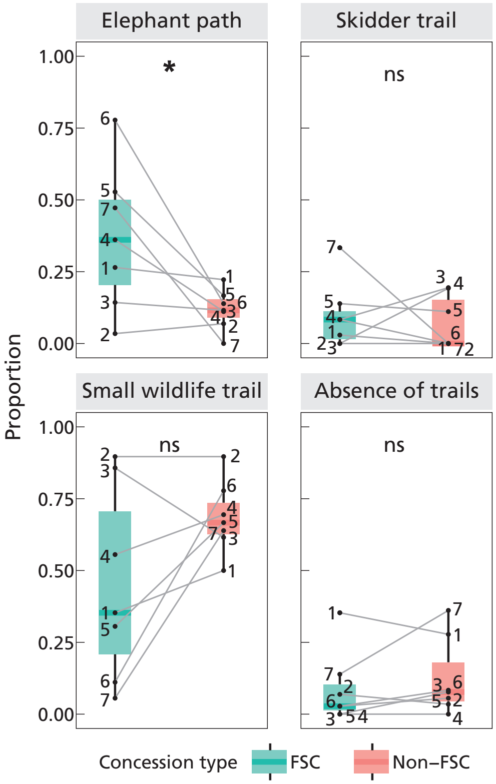


Figure S6. The presence of trails or paths in the field of view between randomly placed cameras in FSC-certified and non-FSC concessions, expressed in proportions. Each camera trap installation location was characterized as either an elephant path, skidder trail, small wildlife trail or as an absence of trail. Only elephant paths were more often encountered in FSC-certified concessions than in non-FSC concessions, while the presence or absence of other types of trails was equivalent between the two forest management types. Camera trap sites were selected as the closest location from the predetermined GPS locations with both a suitable tree and a minimum of four metres visibility . Following this method, randomly encountering more elephant paths is in itself an indication of higher elephant abundances in FSC-certified sites. Numbers in the plot represent paired FSC-certified and non-FSC concessions linked by grey lines. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank test, *: p <= 0.05, ns: p > 0.05.

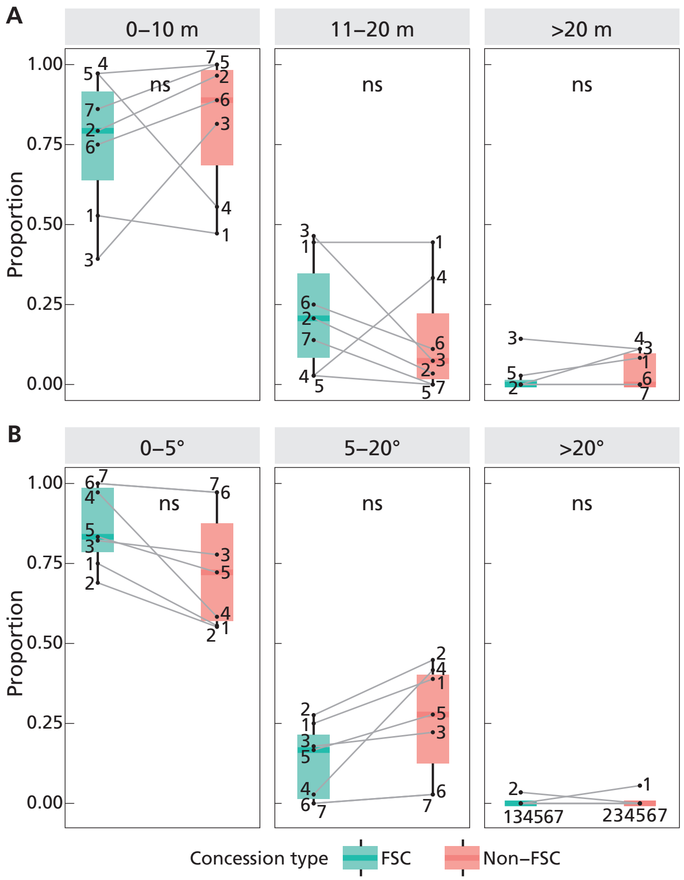


Figure S7. The distributions of three categories of (A) visibility and (B) slope, expressed in proportions, did not differ significantly between camera locations in FSC-certified and non-FSC concessions. Numbers in the plot represent paired FSC-certified and non-FSC concessions linked by grey lines. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank test, ns: p > 0.05.

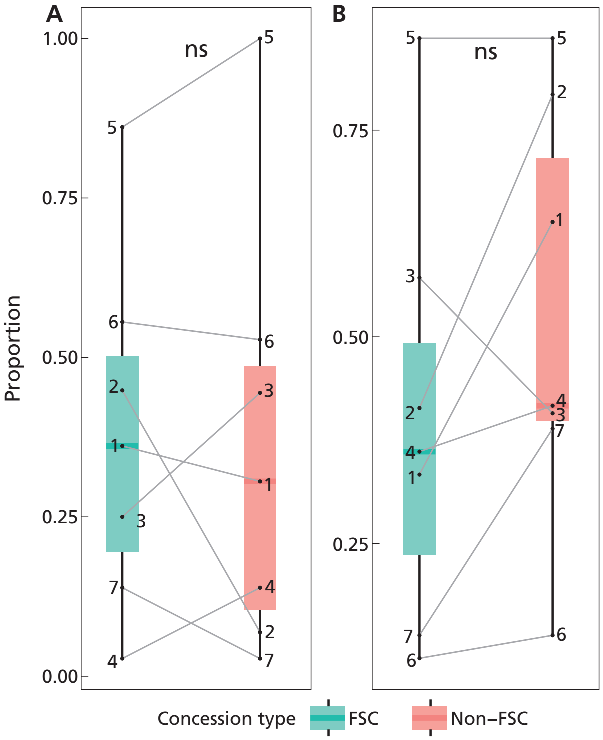


Figure S8. Distributions of (A) fruiting trees within 30 m and (B) small water courses within 50 m distance, expressed in proportions, did not differ significantly at camera trap installation locations in FSC-certified and non-FSC concessions. Numbers in the plot represent paired FSC-certified and non-FSC concessions linked by grey lines. Boxplot whiskers reflect 1.5*IQR. Wilcoxon signed-rank test, ns: p > 0.05.

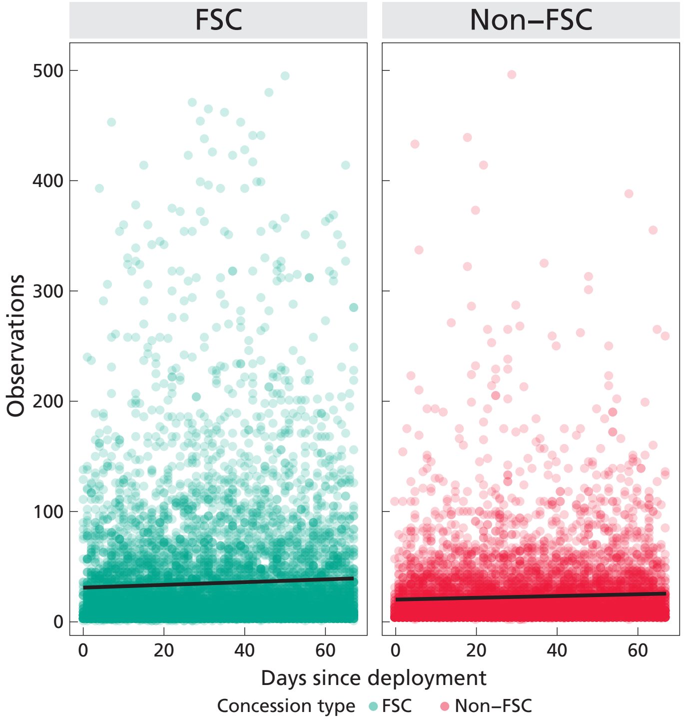


Figure S9. The number of observations over time did not differ significantly between FSC-certified and non-FSC concessions. This analysis explored whether variation in animal shyness over time influences detection. Shyness towards non-natural objects like camera traps may fade over time but we did not find support for this, nor for an effect of management type on the number of observations over time. Linear model: $p > 0.05$.

Table S1. Principles and criteria of the FSC International Standard related to wildlife conservation. For a complete overview of all principles and criteria, as well as verifiers and indicators, see the FSC international standard, 2015.

Description of relevant principles and criteria
1) Compliance with Laws - The Organization shall comply with all applicable laws, regulations and nationally-ratified international treaties, conventions and agreements. 1.4) The Organization shall develop and implement measures, and/or shall engage with regulatory agencies, to systematically protect the Management Unit from unauthorized or illegal resource use, settlement and other illegal activities. 1.5) The Organization shall comply with the applicable national laws, local laws, ratified international conventions and obligatory codes of practice, relating to the transportation and trade of forest products within and from the Management Unit, and/or up to the point of first sale.
6) The Organization shall maintain, conserve and/or restore ecosystem services and environmental values of the Management Unit, and shall avoid, repair or mitigate negative environmental impacts. 6.4) The Organization shall protect rare species and threatened species and their habitats in the Management Unit through conservation zones, protection areas, connectivity and/or (where necessary) other direct measures for their survival and viability. These measures shall be proportionate to the scale, intensity and risk of management activities and to the conservation status and ecological requirements of the rare and threatened species. The Organization shall take into account the geographic range and ecological requirements of rare and threatened species beyond the boundary of the Management Unit, when determining the measures to be taken inside the Management Unit. 6.6) The Organization shall effectively maintain the continued existence of naturally occurring native species and genotypes, and prevent losses of biological diversity, especially through habitat management in the Management Unit. The Organization shall demonstrate that effective measures are in place to manage and control hunting, fishing, trapping and collecting.
7) The Organization shall have a management plan consistent with its policies and objectives and proportionate to scale, intensity and risks of its management activities. The management plan shall be implemented and kept up to date based on monitoring information in order to promote adaptive management. The associated planning and procedural documentation shall be sufficient to guide staff, inform affected stakeholders and interested stakeholders and to justify management decisions. 7.1) The Organization shall, proportionate to scale, intensity and risk of its management activities, set policies (visions and values) and objectives for management, which are environmentally sound, socially beneficial and economically viable. Summaries of these policies and objectives shall be incorporated into the management plan, and publicized.
8) The Organization shall demonstrate that, progress towards achieving the management objectives, the impacts of management activities and the condition of the Management Unit, are monitored and evaluated proportionate to the scale, intensity and risk of management activities, in order to implement adaptive management. 8.2) The Organization shall monitor and evaluate the environmental and social impacts of the activities carried out in the Management Unit, and changes in its environmental condition.

Table S1 continued

Description of relevant principles and criteria
9) The Organization shall maintain and/or enhance the High Conservation Values in the Management Unit through applying the precautionary approach. 9.1) The Organization, through engagement with affected stakeholders, interested stakeholders and other means and sources, shall assess and record the presence and status of the following High Conservation Values in the Management Unit, proportionate to the scale, intensity and risk of impacts of management activities, and likelihood of the occurrence of the High Conservation Values: HCV 1 - Species diversity. Concentrations of biological diversity including endemic species, and rare, threatened or endangered species, that are significant at global, regional or national levels. HCV 2 - Landscape-level ecosystems and mosaics. Intact forest landscapes and large landscape-level ecosystems and ecosystem mosaics that are significant at global, regional or national levels, and that contain viable populations of the great majority of the naturally occurring species in natural patterns of distribution and abundance. HCV 3 - Ecosystems and habitats. Rare, threatened, or endangered ecosystems, habitats or refugia. HCV 4 - Critical ecosystem services. Basic ecosystem services in critical situations, including protection of water catchments and control of erosion of vulnerable soils and slopes. HCV 5 - Community needs. Sites and resources fundamental for satisfying the basic necessities of local communities or Indigenous Peoples (for livelihoods, health, nutrition, water, etc.), identified through engagement with these communities or Indigenous Peoples. HCV 6 - Cultural values. Sites, resources, habitats and landscapes of global or national cultural, archaeological or historical significance, and/or of critical cultural, ecological, economic or religious/sacred importance for the traditional cultures of local communities or Indigenous Peoples, identified through engagement with these local communities or Indigenous Peoples.
10) Management activities conducted by or for The Organization for the Management Unit shall be selected and implemented consistent with The Organization's economic, environmental and social policies and objectives and in compliance with the Principles and Criteria collectively. 10.10) The Organization shall manage infrastructural development, transport activities and silviculture so that water resources and soils are protected, and disturbance of and damage to rare and threatened species, habitats, ecosystems and landscape values are prevented, mitigated and/or repaired.

Table S2. National criteria and indicators of the FSC standards of Gabon and The Republic of Congo regarding hunting. Comparable indicators and criteria are highlighted with numbers in superscript. For a complete overview of all principles and criteria, as well as verifiers and indicators, see the FSC National Forest Stewardship Standard of The Gabonese Republic (2020) and The Republic of Congo (2020).

Gabon	Republic of Congo
Indicator 1.4.1[1] Measures are implemented to provide protection from unauthorized or illegal harvesting, hunting, fishing, trapping, collecting, settlement and other unauthorized activities, notably: 1) Security gates on main forest roads and/ or control of access to high-risk areas; 2) Closure of temporal roads after harvesting; 3) Surveillance patrols on forest road to detect and report to the forest administration, any illegal access to the forest; and 4) Designation of personnel and resources to rapidly detect and monitor illegal activities.	Indicator 1.4.1[1] Measures are implemented to provide protection from unauthorized or illegal harvesting, hunting, fishing, trapping, collecting, settlement and other unauthorized activities, notably: 1) security gates on main forest roads and/ or control of access to high-risk areas; 2) closure of temporal roads after harvesting; 3) surveillance patrols on forest road to detect and prevent illegal access to the forest; and 4) designation of personnel and resources to rapidly detect and monitor illegal activities during the exercise of legal user rights.
Indicator 6.4.4[2&7] The Organization puts in place mechanisms to ensure that: 1) hunting, trapping and fishing are prevented in accordance with applicable regulations; 2) Applicable national and/or international regulations on protection, hunting, fishing and trade in animal species or parts (trophies) are known and complied with; 3) there are internal regulations prohibiting and penalizing illegal hunting, fishing and collecting within the MU, and the transport and trade in bush meat and firearms in the concession-holder's vehicles; 4) there are internal procedures to control illegal hunting, fishing and collecting practices within the Management Unit.	
Criterion 6.6[3] The Organization shall effectively maintain the continued existence of naturally occurring native species and genotypes, and prevent losses of biological diversity, especially through habitat management in the Management Unit. The Organization shall demonstrate that effective measures are in place to manage and control hunting, fishing, trapping and collecting.	Criterion 6.6[3] The Organization shall effectively maintain the continued existence of naturally occurring native species and genotypes, and prevent losses of biological diversity, especially through habitat management in the Management Unit. The Organization shall demonstrate that effective measures are in place to manage and control hunting, fishing, trapping and collecting.
Indicator 6.6.4[4] Effective measures are taken to manage and control hunting, fishing, trapping and collecting activities to ensure that naturally occurring native species, their diversity within species and their natural distribution are maintained.	Indicator 6.6.4[4] Effective measures are taken, and personnel appointed, to manage and control hunting, fishing, trapping and collecting activities to ensure that the diversity and natural distribution of native species is maintained.
Indicator 6.6.5[5] A system of regular and punctual controls is implemented to ensure hunting policies are respected.	Indicator 6.6.5[2] Mechanisms for wildlife protection are in place: Applicable national and/or international regulations on protection, hunting and trade in animal species or parts (trophies) shall be known and complied with.

Table S2 continued

Gabon	Republic of Congo
Indicator 6.6.6[6] Effective mitigation measures are in place to ensure that workers do not increase the practice of hunting, trapping or collecting of bush meat or wild fish.	Indicator 6.6.6[7] There is an internal regulation banning and punishing the transportation of and trade in bush meat, firearms, munitions and hunters in the vehicles belonging to The Organization and its sub-contractors, and governing the keeping of firearms on The Organization's premises. This regulation shall be known, disseminated and complied with.
	Indicator 6.6.7[5] A system of regular and punctual controls to ensure hunting policies are respected is implemented.
	Indicator 6.6.8[6] Effective mitigation measures are in place to regulate the practices of hunting, trapping or collecting of bush meat or wild fish by the workers of The Organization.

Table S3. Camera trap deployment sites and periods. The number of cameras was defined as the number of cameras that were deployed in a concession. The period of deployment was noted as the month and year that the first camera trap was placed, and last camera trap was recuperated. The total deployment time was calculated by taking the sum of all active camera trap days per site. The effort is the total deployment time of a site minus the time camera traps were malfunctioning or covered by vegetation. All sites were deployed for two to three months with one exception where Covid travel restrictions resulted in the cameras remaining in place for longer. The companies are not named to assure anonymity: this was a prerequisite for several companies to participate in the study.

Pair	Country	Type	Number of cameras	Deployment period	Total deployment time (days)	Effort (days)
1	Gabon	FSC	36	Dec 2018 – Mar 2019	2,597	2,453
1	Gabon	Non-FSC	36	Nov 2018 – Mar 2019	1,960	1,960
2	Gabon	Non-FSC	29	Apr 2019 – Jul 2019	2,128	2,128
2	Gabon	FSC	29	Mar 2019 – Jun 2019	2,070	2,030
3	Gabon	Non-FSC	28	Apr 2019 – Jul 2019	1,264	1,258
3	Gabon	FSC	28	Mar 2019 - Jun 2019	1,172	1,087
4	Gabon	FSC	36	Jul 2019 – Oct 2019	3,041	3,007
4	Gabon	Non-FSC	36	Jun 2019 - Oct 2019	3,071	2,962
5	Gabon	FSC	36	Oct 2019 – Jan 2020	2,186	2,148
5	Gabon	Non-FSC	36	Nov 2019 – Jan 2020	2,092	2,087
6	Congo	FSC	36	Mar 2020 – Oct 2020	5,277	4,554
6	Congo	Non-FSC	36	Feb 2020 – Oct 2020	5,558	5,208
7	Congo	FSC	36	Mar 2021 – Jun 2021	2,537	2,532
7	Congo	Non-FSC	36	Mar 2021 – Jun 2021	2,132	2,132
Total			474		37,085	35,546
Average per site			34		2,649	2,539

Table S4. Observed mammals. Encounter rates of observed mammals in FSC-certified and non-FSC concessions, ranked in descending order of encounter rate in FSC-certified concessions. Per certification type the highest encounter rate is depicted in bold. Weight for weight classes (<2 kg, 2-10 kg, 10-30 kg, 30-100 kg, >100 kg) was retrieved from Kingdon (2015). IUCN Red List category was retrieved from the IUCN Red List (IUCN, 2021). IUCN abbreviations: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern. * = Have less than 10 observations and are therefore not included as separate taxonomic groups in the taxonomy analysis.

Species names	Taxonomy	Weight (kg)	Weight class	IUCN	Mean encounter rate FSC (± SEM)	Mean encounter rate non-FSC (± SEM)
Cephalophus callipygus	Even-toed ungulates	21.35	3	LC	0.322 (± 0.138)	0.065 (± 0.026)
Philantomba monticola	Even-toed ungulates	6.25	2	LC	0.229 (± 0.036)	0.285 (± 0.048)
Squirrels	Rodents	0.27	1	LC	0.186 (± 0.022)	0.158 (± 0.033)
Atherurus africanus	Rodents	3.25	2	LC	0.105 (± 0.027)	0.117 (± 0.012)
Mice and shrews	Rodents	0.010	1	LC	0.083 (± 0.027)	0.097 (± 0.037)
Potamochoerus porcus	Even-toed ungulates	80	4	LC	0.082 (± 0.044)	0.018 (± 0.005)
Cephalophus dorsalis	Even-toed ungulates	19.75	3	NT	0.077 (± 0.032)	0.034 (± 0.009)
Cephalophus ogilbyi	Even-toed ungulates	17	3	LC	0.075 (± 0.053)	0.023 (± 0.015)
Cricetomys emini	Rodents	1.2	1	LC	0.067 (± 0.033)	0.092 (± 0.031)
Loxodonta cyclotis	Elephants	2150	5	CR	0.066 (± 0.012)	0.015 (± 0.005)
Cephalophus indet	Even-toed ungulates	18.32	3	LC	0.062 (± 0.018)	0.033 (± 0.013)
Cephalophus silvicultor	Even-toed ungulates	62.5	4	NT	0.041 (± 0.014)	0.008 (± 9.44e-04)
Mandrillus sphinx	Primates	18.5	3	VU	0.031 (± 0.015)	0.019 (± 0.010)
Rats	Rodents	0.14	1	LC	0.027 (± 0.017)	0.060 (± 0.029)
Genetta servalina	Carnivores	1.85	1	LC	0.026 (± 0.006)	0.021 (± 0.005)
Bdeogale nigripes	Carnivores	2.75	2	LC	0.021 (± 0.005)	0.009 (± 0.003)
Hyemoschus aquaticus	Even-toed ungulates	10.85	3	LC	0.021 (± 0.008)	0.011 (± 0.006)
Pan troglodytes	Primates	31.5	4	EN	0.019 (± 0.006)	0.011 (± 0.003)
Xenogale naso	Carnivores	3.6	2	LC	0.019 (± 0.013)	0.007 (± 0.002)
Atilax paludinosus	Carnivores	3.5	2	LC	0.014 (± 0.006)	0.006 (± 0.002)
Cephalophus leucogaster	Even-toed ungulates	17.5	3	NT	0.012 (± 0.003)	0.002 (± 8.27e-04)
Gorilla gorilla	Primates	116.5	5	CR	0.010 (± 0.003)	0.004 (± 0.001)
Cephalophus nigrifrons	Even-toed ungulates	16	3	LC	0.008 (± 0.005)	4.02e-04 (± 4.02e-04)
Cercocebus agilis	Primates	7.83	2	LC	0.008 (± 0.005)	0.002 (± 0.002)
Caracal aurata	Carnivores	10.1	3	VU	0.006 (± 0.002)	6.84e-04 (± 2.12e-04)
Nandinia binotata	Carnivores	2.6	2	LC	0.005 (± 0.001)	0.007 (± 0.002)

Table S4 continued

Species names	Taxonomy	Weight (kg)	Weight class	IUCN	Mean encounter rate FSC (± SEM)	Mean encounter rate non-FSC (± SEM)
Panthera pardus	Carnivores	53.25	4	VU	0.004 (± 0.001)	0.002 (± 6.14e-04)
Phataginus tricuspis	Pangolins	2.3	2	EN	0.004 (± 0.002)	0.004 (± 0.002)
Crossarchus platycephalus	Carnivores	1.25	1	LC	0.004 (± 0.002)	0.006 (± 0.002)
Cercocebus torquatus	Primates	8.13	2	EN	0.003 (± 0.003)	0.002 (± 0.002)
Phataginus tetradactyla	Pangolins	2.9	2	VU	0.002 (± 8.49e-04)	0.004 (± 0.001)
Smutsia gigantea	Pangolins	32.5	3	EN	0.002 (± 4.07e-04)	0.001 (± 4.12e-04)
Cercopithecus nictitans	Primates	5.53	2	NT	0.001 (± 7.86e-04)	3.62e-04 (± 3.32e-04)
Syncerus caffer	Even-toed ungulates	637.5	5	NT	8.52e-04 (± 3.98e-04)	7.05e-04 (± 3.32e-04)
Civettictis civetta	Carnivores	13.5	3	LC	6.38e-04 (± 5.10e-04)	0
Orycteropus afer	Tubulidentata*	61	4	LC	5.55e-04 (± 5.20e-04)	0
Cercopithecus indet	Primates	4.13	2	NT	4.43e-04 (± 3.90e-04)	1.91e-04 (± 1.04e-04)
Euoticus elegantulus	Primates	0.32	1	LC	4.39e-04 (± 2.11e-04)	4.59e-04 (± 4.05e-04)
Mellivora capensis	Carnivores	9.85	2	LC	3.97e-04 (± 2.73e-04)	0
Lophocebus albigena	Primates	7	2	VU	2.26e-04 (± 2.26e-04)	0
Poiana richardsonii	Carnivores	0.60	1	LC	1.88e-04 (± 1.41e-04)	0
Tragelaphus spekii	Even-toed ungulates	69	4	LC	1.57e-04 (± 1.57e-04)	0.001 (± 0.001)
Tragelaphus eurycerus	Even-toed ungulates	275.75	5	NT	1.25e-04 (± 1.25e-04)	0
Dendrohyrax dorsalis	Hyracoidea*	3.15	2	LC	1.18e-04 (± 7.81e-05)	0
Cercopithecus cephus	Primates	3.35	2	LC	8.96e-05 (± 6.14e-05)	7.81e-04 (± 2.91e-04)
Arctocebus aureus	Primates	0.235	1	LC	7.89e-05 (± 5.24e-05)	9.65e-05 (± 9.65e-05)
Aonyx congicus	Carnivores	20	3	NT	5.64e-05 (± 5.64e-05)	0
Thryonomys swinderianus	Rodents	4.35	2	LC	3.14e-05 (± 3.14e-05)	5.49e-05 (± 5.49e-05)
Hylochoerus meinertzhageni	Even-toed ungulates	178.75	5	LC	0	2.54e-04 (± 2.24e-04)
Galagoides thomasi	Primates	0.10	1	LC	0	1.15e-04 (± 7.59e-05)
Perodicticus potto	Primates	1.2	1	NT	0	8.23e-05 (± 8.23e-05)
Sciurocheirus gabonensis	Primates	0.26	1	LC	0	4.82e-05 (± 4.82e-05)
Cercopithecus pogonias	Primates	3.53	2	NT	0	2.74e-05 (± 2.74e-05)
Colobus guereza	Primates	9.28	2	LC	0	2.74e-05 (± 2.74e-05)
Colobus satanas	Primates	9.9	2	VU	0	2.74e-05 (± 2.74e-05)

Table S5. Overview of the statistical analyses and descriptive statistics of mammal encounter rates in paired FSC-certified and non-FSC concessions. Bold: $p < 0.05$, Underscore: $p < 0.1$.

Grouping variable and statistical test	Grouping classes	Test statistic and uncorrected p-values	Test statistic and Holm corrected p-values	FSC median encounter rate and IQR	Non-FSC median encounter rate and IQR
Total encounter rate (Wilcoxon signed-rank)	-	**V = 26, p = 0.047**	-	1.53 (0.36)	1.07 (0.40)
Weight, overall (Friedman test)	-	**Friedman, X2(4) = 13, p = 0.011**	-	-	-
Weight, pairwise comparisons (Wilcoxon signed-rank)	>100 kg	**V = 27, p = 0.031**	V = 27, p = 0.125	0.076 (0.044)	0.019 (0.015)
	30-100 kg	**V = 28, p = 0.016**	V = 28, p = 0.078	0.088 (0.126)	0.048 (0.030)
	10-30 kg	V = 25, p = 0.078	V = 25, p = 0.234	0.473 (0.275)	0.165 (0.126)
	2-10 kg	V = 11, p = 0.688	V = 11, p = 1	0.393 (0.192)	0.451 (0.176)
	<2 kg	V = 11, p = 0.688	V = 11, p = 1	0.369 (0.177)	0.400 (0.349)
IUCN Red List categories, overall (Friedman test)	-	**Friedman, X2(2) = 10.9, p = 0.028**	-	-	-
IUCN Red List categories, pairwise comparisons (Wilcoxon signed-rank)	Critically Endangered (CR)	**V = 27, p = 0.031**	V = 27, p = 0.157	0.075 (0.044)	0.018 (0.015)
	Endangered (EN)	V = 20, p = 0.375	V = 20, p = 0.750	0.025 (0.024)	0.018 (0.009)
	Vulnerable (VU)	V = 24, p = 0.578	V = 24, p = 0.750	0.024 (0.074)	0.012 (0.031)
	Near Threatened (NT)	V = 23, p = 0.156	V = 23, p = 0.468	0.085 (0.061)	0.038 (0.030)
	Least Concern (LC)	V = 18, p = 0.109	V = 18, p = 0.436	1.307 (0.405)	0.993 (0.386)
Taxonomy, overall (Friedman test)	-	**Friedman, X2(5) = 22.6, p < 0.001**	-	-	-
Taxonomy, pairwise comparisons: Wilcoxon signed-rank	Elephants	**V = 28 , p = 0.016**	V = 28, p = 0.094	0.0591 (0.026)	0.0127 (0.011)
	Primates	**V = 27, p = 0.031**	V = 27, p = 0.157	0.0785 (0.013)	0.0326 (0.033)
	Even-toed Ungulates	V = 25, p = 0.078	V = 25, p = 0.312	0.7960 (0.497)	0.5217 (0.119)
	Carnivores	V = 21, p = 0.297	V = 21, p = 0.891	0.0690 (0.037)	0.0551 (0.018)
	Pangolins	V = 13, p = 0.938	V = 13, p = 1	0.0067 (0.004)	0.0066 (0.006)
	Rodents	V = 12, p = 0.813	V = 12, p = 1	0.4337 (0.243)	0.5395 (0.270)
Forest antelopes by size (Wilcoxon signed-rank)	Yellow-backed duiker ~62 kg	**V = 28, p = 0.0156**	**V = 28, p = 0.0468**	0.025 (0.040)	0.008 (0.002)
	Red duikers ~18 kg	**V = 26, p = 0.0469**	V = 26, p = 0.0938	0.454 (0.315)	0.159 (0.139)
	Blue duiker ~6 kg	V = 7, p = 0.297	V = 7, p = 0.297	0.243 (0.146)	0.261 (0.149)
Carnivores by size (Wilcoxon signed-rank)	>10 kg	**V = 28, p = 0.0156**	**V = 28, p = 0.0312**	0.011 (0.004)	0.002 (0.003)
	<10 kg	V = 21, p = 0.2970	V = 21, p = 0.2970	0.057 (0.042)	0.055 (0.016)

Table S5 continued

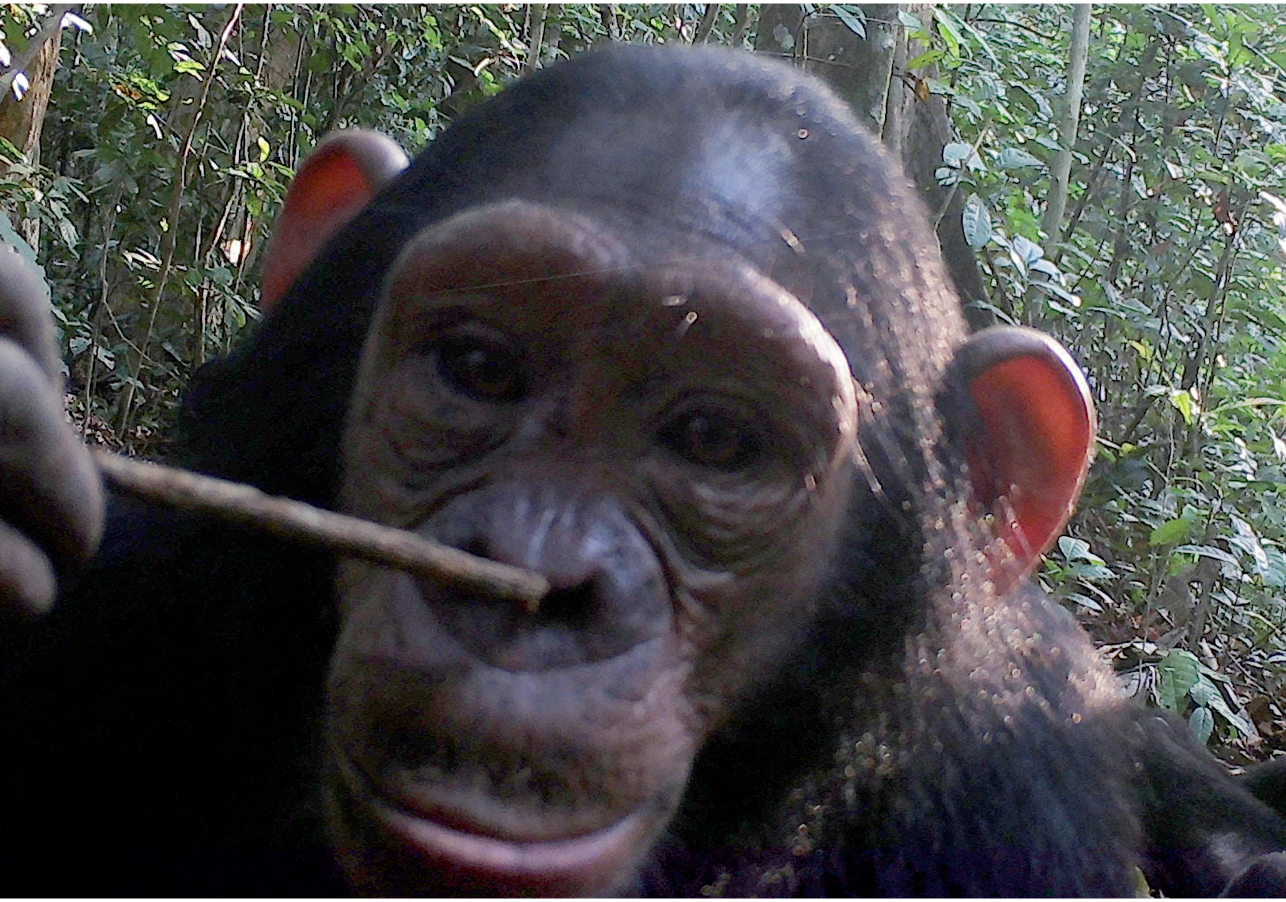
Grouping variable and statistical test	Grouping classes	Test statistic and uncorrected p-values	Test statistic and Holm corrected p-values	FSC median encounter rate and IQR	Non-FSC median encounter rate and IQR
Primates by size (Wilcoxon signed-rank)	Apes >30 kg	V = 23 , p = 0.156	V = 23, p = 0.312	0.024 (0.038)	0.010 (0.008)
	Monkeys <20 kg	V =23 , p = 0.156	V = 23, p = 0.312	0.039 (0.047)	0.015 (0.020)
Pangolins by size (Wilcoxon signed-rank)	>25 kg	V = 17, p = 0.688	V = 17, p = 1	0.002 (0.001)	0.001 (0.002)
	<5 kg	V = 13, p = 0.938	V = 13, p = 1	0.005 (0.007)	0.006 (0.007)
Total faunal biomass (Wilcoxon signed-rank)	-	**V = 28, p = 0.016**	-	161.55 (47.91)	36.27 (27.54)

Table S6. Overview of the statistical analyses and descriptive statistics of covariates in FSC-certified and non-FSC concessions. Bold: p < 0.05, Underscore: p < 0.1.

Covariate type	Covariate	Test statistic and uncorrected p-values (Wilcoxon signed-rank tests)	Test statistic and Holm corrected p-values (Wilcoxon signed-rank tests)	FSC medians and IQR	Non-FSC medians and IQR
Hunting signs (in proportions)	-	**V = 26, p = 0.036**	-	0 (0.045)	0.139 (0.245)
Geographic covariates	Distance to roads (m)	V = 9, p = 0.469	-	4063 (4587)	7336 (3558)
	Distance to rivers (m)	V = 17, p = 0.688	-	4259 (6998)	5355 (2813)
	Distance to human settlements (m)	V = 13, p = 0.938	-	8304 (12436)	12334 (3395)
	Distance to protected areas (m)	V = 17, p = 0.688	-	57372 (30014)	37341 (33290)
	Elevation (m)	V = 12, p = 0.81	-	474 (122)	380 (235)
The presence of trails or paths (in proportions)	Elephant path	**V = 28, p = 0.016**	V = 28, p = 0.062	0.361 (0.296)	0.115 (0.063)
	Skidder trail	V = 12, p = 0.833	V = 12, p = 1	0.083 (0.096)	0 (0.152)
	Small wildlife trail	V = 4, p = 0.109	V = 4, p = 0.327	0.353 (0.498)	0.667 (0.109)
	Absence of trails	V = 8, p = 0.675	V = 8, p = 1	0.028 (0.090)	0.077 (0.136)
Camera trap site visibility (in proportions)	0-10 m	V = 9, p = 0.469	V = 9, p = 1	0.793 (0.278)	0.889 (0.298)
	11-20 m	V = 20, p = 0.375	V = 20, p = 1	0.207 (0.264)	0.074 (0.205)
	>20m	V = 1, p = 0.414	V = 1, p = 1	0 (0.014)	0 (0.097)
Camera trap site slope (in proportions)	0-5°	V = 15, p = 0.402	V = 15, p = 0.804	0.833 (0.2)	0.722 (0.306)
	5-20°	V = 4, p = 0.208	V = 4, p = 0.624	0.167 (0.2)	0.278 (0.278)
	>20°	V = 1, p = 1	V = 1, p = 1	0	0
Presence of fruiting trees within 30 m		V = 13.5, p = 1	-	0.361 (0.307)	0306 (0.382)
Presence of small water courses within 50 m		V = 3, p = 0.142	-	0.361 (0.256)	0.417 (0.318)

Table S7. Grouping variables and classes. The numbers between brackets indicate the number of species per class.

Grouping variables	Classes
Weight class	>100 kg (5) / 30-100 kg (7) / 10-30 kg (11) / 2-10 kg (20) / <2 kg (13)
IUCN Red List category	Critically Endangered (CR) (2) / Vulnerable (VU) (6) / Near Threatened (NT) (10) / Endangered (EN) (4) / Least Concern (LC) (34)
Taxonomic group	Elephants (1) / Primates (17) / Even-toed ungulates (14) / Carnivores (12) / Pangolins (3) / Rodents (6)
Forest antelopes (duikers) by size	Large (~62 kg); Yellow-backed duiker (Cephalophus silvicultor) (1) / Medium (~18 kg); Red duikers (Cephalophus callipygus, Cephalophus dorsalis, Cephalophus leucogaster, Cephalophus nigrifrons, Cephalophus ogilbyi and Cephalophus indet) (6) / Small (~6 kg); Blue duiker (Philantomba monticola) (1)
Carnivores by size	>10 kg (4) / <10 kg (8)
Primates by size	Apes >30 kg (2) / Monkeys <20 kg (15)
Pangolins by size	>25 kg (1) / <5 kg (2)



A curious chimpanzee uses a stick to inspect a camera trap.

Chapter 4

Introducing a Central African Primate Vocalization Dataset for Automated Species Classification

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This chapter has been published as a conference paper for the ‘Interspeech 2021’ conference as: Zwerts, J.A., Treep, J., Kaandorp, C.S., Meewis, F., Koot, A.C., Kaya, H. (2021) Introducing a Central African Primate Vocalisation Dataset for Automated Species Classification. Proc. Interspeech 2021, 466-470, doi: 10.21437/Interspeech.2021-154

Abstract

Automated classification of animal vocalizations is a potentially powerful wildlife monitoring tool. Training robust classifiers requires sizable annotated datasets, which are not easily recorded in the wild. To circumvent this problem, we recorded four primate species under semi-natural conditions in a wildlife sanctuary in Cameroon with the objective to train a classifier capable of detecting species in the wild. Here, we introduce the collected dataset, describe our approach and initial results of classifier development. To increase the efficiency of the annotation process, we condensed the recordings with an energy/change based automatic vocalization detection. Segmenting the annotated chunks into training, validation and test sets, initial results reveal up to 82% unweighted average recall (UAR) test set performance in four-class primate species classification.

1. Introduction

Wildlife is declining at unprecedented rates, and monitoring trends in biodiversity is key to engage in effective conservation actions (Almond et al., 2020). Using acoustic recordings to identify and count species is a promising non-invasive and cost-effective monitoring tool (Sugai et al., 2019). This can be particularly useful in environments with limited visibility such as tropical forests, or for arboreal, shy or nocturnal species that are more easily heard than seen. Acoustic monitoring, especially in conjunction with other monitoring methods, has the potential to profoundly change ecological research by opening up new ways of studying community composition, species interactions and behavioral processes (Buxton et al., 2018). For efficient analysis of audio recordings however, automated detection is pivotal. In addition to relieving a data processing bottleneck, machine learning methods allow for consistency in terms of quality, increasing the comparability and reproducibility of the output.

Training robust classifiers requires sizable amounts of annotated data, which can require substantial efforts to compile from natural forest recordings. To circumvent this problem, we recorded several primate species in a sanctuary in Cameroon, including chimpanzees (*Pan troglodytes*, n=20), mandrills (*Mandrillus sphinx*, n=17), red-capped mangabeys (*Cercocebus torquatus*, n=6) and a mixed group of guenon species (*Cercopithecus spp.*, n=20). The primates in the sanctuary live in semi-natural conditions with background noise that is somewhat, although not wholly, comparable to natural background noise. The ultimate objective of these efforts is to train a classifier capable of detecting species in the wild. This may also provide insights into whether this approach, of using sanctuary recordings, can be used to train classifiers for other species as well, to aid in the development of cost-effective monitoring to meet modern conservation challenges. In this paper, we present the dataset, the semi-automatic annotation process that we used to speed up the manual annotation process, and a benchmark species classification system.

1.1. Related Work

Multiple studies have applied automatic acoustic monitoring for a variety of taxa including cetaceans (Bittle & Duncan, 2013), birds (Priyadarshani et al., 2018), bats (Russo & Voigt, 2016), insects (Ganchev & Potamitis, 2007), amphibians (Brauer et al., 2016), and forest elephants (Wrege et al., 2017). However, they have so far only been sporadically been used for primates (Clink et al., 2019; Enari et al., 2019; Fedurek et al., 2016; Heinicke et al., 2015; Mielke & Zuberbühler, 2013; Turesson et al., 2016). A brief summary of recent works on classification of primate vocalizations is given in Table 1. We observe that Mel-Frequency Cepstral Coefficients (MFCC) are commonly used in classifying primate vocalizations, in most cases without other acoustic descriptors. In our study, we also use MFCCs (together with temporal delta coefficients) and combine them with RASTA-style Perceptual Linear Prediction Cepstral Coefficients. There are also off-the-shelf applications like Kaleidoscope Pro (Wildlife Acoustics, MA, USA) based on Hidden Markov Models that were used in recent works for call type classification of Japanese macaques (*Macaca fuscata*) (Enari et al., 2019).

2. Central African Primate Dataset

2.1. Acoustic Data Collection

The acoustic data is collected in the Mefou Primate Sanctuary (Ape Action Africa) in Cameroon in December 2019 and January 2020. The sanctuary, which houses the primates in a seminatural forest setting, cares for rescued primates and engages in conservation and education initiatives. Recordings were made using Audiomoth (v1.1.0) recorders (Hill et al., 2019). Devices recorded 1min segments continuously at 48 kHz and 30.6 dB gain, storing the data in one minute WAVE-files, with interruptions from two to five seconds between recordings for the recorder to save the files. For all species, the recorders were installed either directly on the fence of their respective enclosures, or maximally up to 3 meters away from it. Per species, the enclosures differed in size and were approximately 40 × 40 meters in size for the guenons and red-capped mangabeys, 50 × 50 meters for the mandrills and 70 × 70 meters for the chimpanzees. Distance between the recorder and the animals naturally varied depending on the location of the animal within the enclosure. The smallest distance between two enclosures having different species was 30 meters. Due to the limited distance between some of the enclosures and the loudness of the vocalizations, some level of interference (i.e. the existence of a distant call of an unintended species) between the species' vocalizations is present, particularly in the mandrill recordings. Recordings can also contain noise from dogs, humans talking, or other human activities. The chimpanzees were recorded in two separate enclosures with two recorders per enclosure recording simultaneously. Hence, there may be overlap in vocalizations for recordings 1 and 2 as well as for recordings 3 and 4. This issue is considered in the chronological ordering based segmentation of the data into the training, validation and test sets. The total dataset amounts to a duration of 1112 hours, 358 GBs of original audio collected over a time span of 32 days.

2.2. Annotation

The first collection of annotations was compiled by manually reviewing the sound recordings and corresponding spectrograms in Raven Pro® software. To speed up this process, we 'condensated' the data with an energy/change based automatic vocaliza-

Table 1. Summary of recent works on automatic primate vocalization classification. k-NN: k-Nearest Neighbors, LPF: Linear Prediction Filter, MLP: Multi-Layer Perceptron, SVM: Support Vector Machines, OPF: Optimum Path Forest, ZCR: Zero Crossing Rate.

Work	Task(s)	Species	Features	Classifiers
Mielke & Zuberbühler, 2013	Three recognition tasks (individual, call type and species)	Blue monkey (Cercopithecus mitis stuhlmanni), Olive baboon (Papio anubis), Redtail monkey (Cercopithecus ascanius schmidti), Guereza colobus (Colobus guereza occidentalis)	MFCC [1-32] and Deltas	MLP
Heinicke et al., 2015	5-class primate classification	Chimpanzee (Pan troglodytes), Diana monkey (Cercopithecus diana), King colobus (Colobus polykomos) and Western red colobus (Procolobus badius)	MFCCs, loudness, spectral crest factor, spectral flatness measure, and ZCR	SVM and GMM
Fedurek et al., 2016	Age, Context, Identity, Social Status	Chimpanzee (Pan troglodytes)	MFCCs	SVM
Turesson et al., 2016	8-class classification of Marmoset vocalizations	Common marmoset (Callithrix jacchus)	LPC with LPF orders of 10, 15, 20 and 25	AdaBoost, Bayesian Classifier, k-NN, Logistic regression, MLP, SVM, Optimum Path Forest
Clink et al., 2019	Distinguishing individuals	Bornean gibbon (Hylobatidae muelleri)	MFCC [1-12]	SVM

tion detection using the first batch of manual annotations to estimate the detection performance. An overview of the semi-automatic annotation process is illustrated in Figure 1. The detection comprises obtaining the power distribution from the power spectrum. From a species-specific frequency sub-band, we collect chunks (time-intervals) in which the registered signal loudness exceeds a species-specific threshold, or in which the local cumulative power distribution deviates from a global counterpart. The species specific thresholds are optimized to include close to all (>95%) initial annotations and to remove as much background sections as possible. The 'condensed'

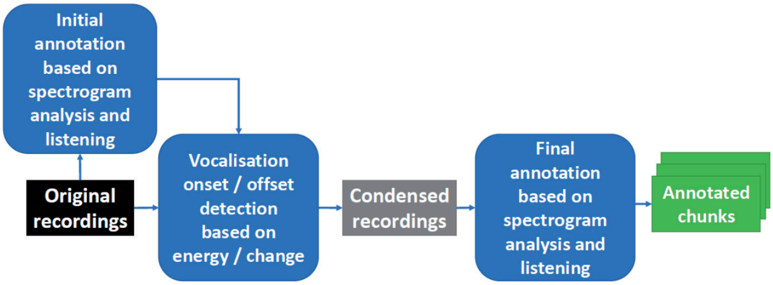


Figure 1. The semi-automatic annotation pipeline used in the study.

collection represents a set of timestamps, where we expect to hear disruptions in the ambient noise. The time-intervals are used to extract the corresponding signal fragments from our raw data. These fragments are bundled into a new audio file containing a high density of vocalizations that can be annotated more efficiently.

Each species produces several vocalization types, each varying in relative frequency, loudness and spectral properties. Experts consider these cues while observing the spectrogram (see Figure 2 for exemplar spectrograms), spotting a candidate chunk and then listening to the selected chunk. This process yields over 10K annotated primate vocalizations with a class distribution of 6652 chimpanzee, 2623 mandrill, 627 red-capped mangabey and 476 of the mixed guenon group.

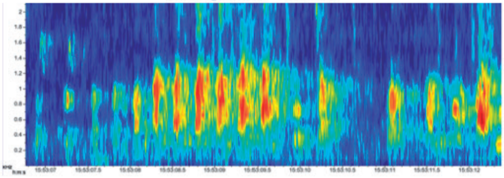
3. Benchmark Vocalization Classification System

To assess how well the species vocalizations can be automatically classified in the presented dataset, we present an acoustic primate classification system. The first stage is acoustic feature extraction, where we extract a standard set of acoustic descriptors from the signal and then summarize them using the statistical functionals (such as mean and standard deviation) over each chunk. This stage produces suprasegmental features of equal length. The next stage is machine learning, where the acoustic features and corresponding primate classes are input to a supervised learner. The details of these stages are given in the subsequent subsections.

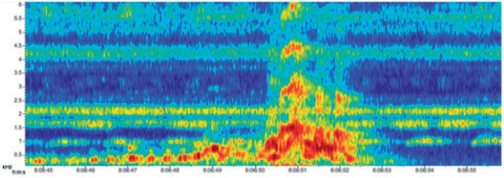
3.1. Acoustic Feature Extraction

As acoustic Low-Level Descriptors (LLDs), we extract Mel-Frequency Cepstral Coefficients (MFCCs) 0-24 and Relative Spectral Transform (RASTA) (Hermansky & Morgan, 1994) - Perceptual Linear Prediction (PLP) (Hermansky, 1990) cepstrum for 12^{th} order linear prediction, together with their first and second order temporal coefficients (Δ and $\Delta\Delta$), making an LLD vector of 114 dimensions. The descriptors are then summarized using 10 functionals, based on the success observed in former paralinguistic studies (Çiftçi et al., 2018; Kaya et al., 2019). The functionals used are: mean, standard deviation, slope and offset from the first order polynomial, the curvature (the leading coefficient) from the second order polynomial fit to the LLD contour, minimum value and its relative position, maximum value and its relative position, zero crossing rate of the LLD contour normalized into [-1,1] range. This process yields $114 \times 10 = 1140$ supra-segmental acoustic features for each chunk, regardless of the number of frames.

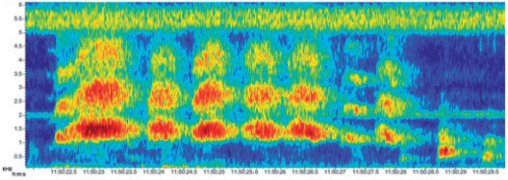
Chimpanzee ‘Grunts’



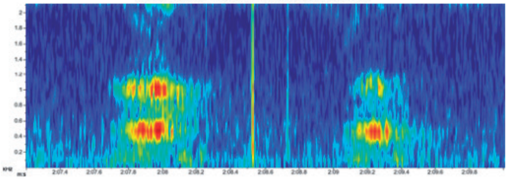
Chimpanzee ‘Pant Hoot’



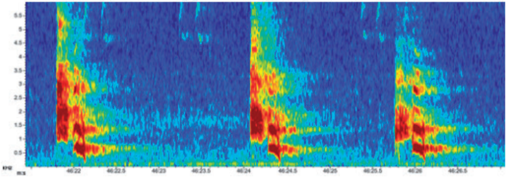
Chimpanzee ‘Screams’



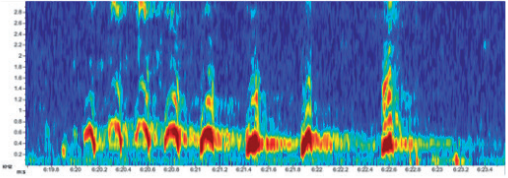
Mandrill ‘Two Phase Grunts’



Red-Capped Mangabey ‘Wahoo’



Red-Capped Mangabey ‘Whoop Gobble’



Guenon spp. ‘Pyow’

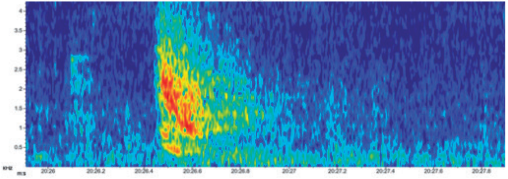


Figure 2. Exemplar spectrograms for different vocalizations of the annotated primate species.

3.2. Model Learning

In our work, we employ Kernel Extreme Learning Machine (ELM) (Huang et al., 2011) method, since this is a fast and accurate algorithm that previously produced state-of-the-art results on several paralinguistic problems (Kaya & Karpov, 2016, 2017). Here, we opt to provide a brief explanation of ELM. Initially, ELM is proposed as a fast learning method for Single Hidden Layer Feedforward Networks (SLFN): an alternative to back-propagation (Huang et al., 2004). To increase the robustness and the generalization capability of ELM, a regularization coefficient **C** is included in the optimization procedure. Therefore, given a kernel **K** and the label vector $\mathbf{T} \in R^{N\times 1}$ where N denotes the number of instances, the projection vector β is learned as follows (Huang et al., 2011):

$$\beta = (\frac{\mathbf{I}}{C} + \mathbf{K})^{-1}\mathbf{T}. \qquad (1)$$

In order to prevent parameter over-fitting, we use the linear kernel $\mathbf{K}(x,y) = x^T y$, where x and y are the (normalized) feature vectors. With this approach, the only parameter of our model is the regularization coefficient C, which we optimize on the validation set.

4. Preliminary Experiments on the Primate vocalization Dataset

In this section we present our spectral analysis and the results of the preliminary classification experiments using the proposed benchmark system.

4.1. Spectral Analysis of vocalizations

During the semi-automatic annotation process, we have analyzed the spectral characteristics of vocalizations and the background noise per species. Based on domain knowledge and initial experimentation, we focused on spectral bands up to 2KHz. For this analysis, we have combined all annotated chunks for each primate class, obtained the power spectrum and then summarized the power in decibels (dB) using mean over time. We applied the same procedure for corresponding background portions for each species. The difference between the two means (see Figure 3) in dB provides an idea about the signal-to-noise ratio (SNR) and as such the relative difficulty of distinguishing each species' vocalizations in the given acoustic background conditions. In the figure, we observe multiple modes for mandrills and red-capped mangabeys, which correspond to different call types (c.f. Figure 2). In line with the acoustic observations during the annotations, vocalizations from mandrills and red-capped mangabeys have lower SNR values, making both the annotation and automated detection a harder problem.

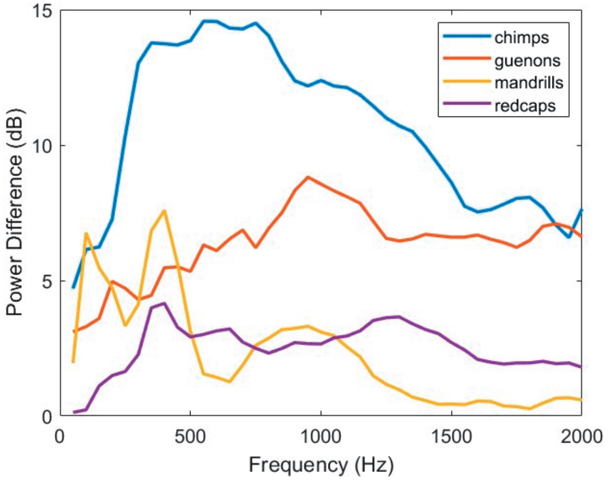


Figure 3. Average power (dB) difference between the mean vocalization (signal) and background (noise) spectrum.

4.2. Classification Results

For the classification experiments, we partitioned the dataset into training, validation and test sets using a temporal ordering (i.e. training correspond to the oldest, test to the newest recordings) with a ratio of 3:1:1, respectively. We set up two classification tasks 1) four-class classification of the species, 2) the four species classes plus the background chunks from the recordings of all species as the fifth class. To generate the background chunks, we sampled from the recordings not annotated as vocalization, to exactly match the duration distribution of the annotated chunks of each species. This makes the five class problem highly imbalanced, as half of the chunks are of background class. However, such an imbalance is not extra-ordinary, if the final aim is to train classifiers for wildlife monitoring.

The models are trained on the training set, optimizing the Kernel ELM complexity hyper-parameter on the validation set. Then using the optimal hyper-parameter, the combination of the training and the validation sets are re-trained, and the corresponding model's predictions are checked against the ground truth test set labels. We use both accuracy and unweighted average recall (UAR), to report the predictive performance.

Using the acoustic features described in Section 3.1, we then trained the Kernel ELM models with z-normalization (ZN - standardizing each feature such that they have zero mean and unit variance) and a combination of ZN with feature-vector level L2 normalization, as suggested in (Kaya et al., 2016). When used with a linear kernel, L2 normalization effectively converts the linear kernel into a cosine similarity kernel. The hyper-parameters of Kernel ELM method is optimized in the set $10^{\{-6,-5,-4,-3,-2,-1,0,1\}}$ with ZN and in in the set $10^{\{-1,0,1,2,3,4,5,6\}}$ with ZN+L2 normalization combination. The respective validation and test performance of the trained models are summarized in Table 2. Note that we optimize for UAR due to class imbalance, while reporting both accuracy and UAR measures.

Table 2. Validation and test set performances of KELM models for four and five-class classification tasks.

		Validation		Test	
Task	Norm	Accuracy	UAR	Accuracy	UAR
Four-cls	ZN	0.554	0.697	0.735	0.821
	ZN+L2	0.595	0.705	0.767	0.823
Five-cls	ZN	0.603	0.610	0.682	0.707
	ZN+L2	0.617	0.627	0.697	0.698

From the table, we observe that the test set (single probe for each normalization option and task combination) performances are always better than the corresponding validation set performance. Moreover, all results are dramatically higher than chance-level UAR, which is 0.25 for the four-class and 0.2 for the five-class classification task. The results show that 1) the collected acoustic recordings have clear distinction for automatic discrimination of primate vocalizations, and 2) the proposed system has a good generalization, reaching test set UAR scores of 0.82 and 0.70 in four-class and five-class classification tasks, respectively.

5. Discussion and Conclusions

Initial results showed that we attain relatively high classification performance using our proposed system combining functionals of MFCC and RASTA-PLPC descriptors and modeling them using Kernel ELM. Data condensation also proved to be a valuable addition to the workflow for reducing the annotation workload. Our future aim is to apply the model on acoustic recordings of natural forests.

Natural forest sounds pose the additional challenge of containing far fewer vocalizations compared to the sanctuary, and significantly higher levels of background noise, in particular in less relevant frequency bands. Moreover, similar to humans, primates can have varying vocal behavior across sex and age, including sex-specific call types, differences in frequency of specific vocalization types, and differences in acoustic structures of shared call types (Mielke & Zuberbühler, 2013; Soltis et al., 2005). There is also some extent of interindividual variation, especially for chimpanzees (Fedurek et al., 2016). Considering the limited group sizes from which we derive our data, such variation may inevitably result in low generalization when applied to the natural variation of individuals and group composition. Finally, not all species and species call types will be equally suitable for automated detection. Louder species such as chimpanzees will be more easily distinguished from background noise than for instance mandrills, and will consequently also have wider detection areas. Chimpanzees, however, often scream simultaneously, making it difficult to distinguish separate calls.

Future work lies in overcoming these challenges, which are partly caused because of the mismatch of acoustic conditions between sanctuary and natural data. Nonetheless, using sanctuary data has the advantage to provide relatively low-cost and accessible training data for classifiers, which may in turn boost the development and increased adoption of semi-automatic acoustic wildlife monitoring methods. To aid this development, the presented dataset is made publicly available in the context of the Interspeech 2021 Computational Paralinguistics Challenge (ComParE 2021) (Schuller et al., 2021).

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Chapter 5

Exploring spatio-temporal variation in soundscape saturation of an African tropical forest landscape

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This chapter has been published in the journal Ecological Indicators as:
Zwerts, J. A., Wiegers, J. Y., Sterck, E. H. M., & van Kuijk, M. (2022). Exploring spatio-temporal variation in soundscape saturation of an African tropical forest landscape. Ecological Indicators, 137, 108712.

Abstract

Monitoring biodiversity calls for efficient monitoring techniques. Soundscape analysis is a landscape-level approach to acoustic monitoring whereby acoustic indices are calculated as proxies for biodiversity based on all sounds occurring in a landscape, i.e. a soundscape. However, it is not fully understood what the influence is of environmental, anthropogenic and temporal heterogeneity on soundscapes and what soundscapes mean in terms of species diversity. Here, we use soundscape saturation, a proxy for acoustic diversity which calculates the degree of use of acoustic niches. We study how soundscape saturation responds to forest management and seasonality in the tropical forests of Gabon, while taking into account distance to rivers, human accessibility, signs of hunting, elevation and slope. To study the contribution of medium to large mammals to soundscape saturation, we relate soundscape saturation to the abundance of several animal guilds as estimated with camera trap data. Soundscape saturation was higher in a multi-use forest vs. logging concessions, in the rainy reason vs. the dry season, and in proximity of rivers and human access points. Elevation, slope, and hunting were less important covariates. We did not find strong evidence for a relationship between soundscape saturation and the abundance of several mammal guilds derived from camera traps. The lack of this relationship highlights the opportunity for a joint approach of eco-acoustics and camera trapping due to complementary species coverage. Our study provides the first soundscape saturation study in African tropical forests and the first to combine soundscape saturation with camera trap data. Soundscape saturation is considered a useful additional index for quantifying biodiversity across a range of land-use types. Future studies may aim to improve species inference and the site-specific interpretation of saturation levels by investigating species-specific contributions to, and spatiotemporal variation in, acoustic activity.

1. Introduction

Human encroachment of natural ecosystems heavily impacts biodiversity (Lewis et al., 2015). Knowledge of our ecosystems and a thorough understanding of how they respond to human activity is fundamental for effective conservation actions (Pereira et al., 2012; Stephenson, 2019). Efficient, scalable biomonitoring methods are a prerequisite for this understanding (Stowell & Sueur, 2020), especially for landscape scale conservation (Reed et al., 2015). One increasingly used approach is soundscape analysis (Alvarez-Berríos et al., 2016; Merchant et al., 2015; Sueur et al., 2014; Sugai et al., 2019), whereby acoustic indices are calculated and used as proxies for biodiversity. These soundscape analyses include all animal sounds emanating from a landscape and cover all vocally active species ranging from insects to elephants (Pijanowski, Farina, et al., 2011).

Acoustic indices are obtained at relatively low cost, are reproducible and objective, and provide a lasting image of the vocal footprint of a landscape. Soundscape analysis offers great potential for landscape level monitoring given its ability to accurately predict biodiversity (Buxton, McKenna, et al., 2018), with applications in measuring the impacts of forest fragmentation (Burivalova et al., 2018), climate change (Krause & Farina, 2016), traffic (Barber et al., 2011; Duarte et al., 2019; Pieretti & Farina, 2013), resource extraction (Burivalova, Purnomo, et al., 2019; Campos-Cerqueira et al., 2019; Deichmann et al., 2017), agro-industrial operations (Furumo & Mitchell Aide, 2019) and conservation (Burivalova, Game, et al., 2019). Other potential applications involve tracking the impacts of reforestation on biodiversity and establishing biodiversity baselines for forest finance schemes. Thus, soundscapes may offer the potential to determine the state of, and track changes in, biodiversity at a landscape scale. Studying the potential applications for soundscape analyses is particularly relevant given the pervasive and increasing human presence in natural systems (Pijanowski et al., 2011) and requires knowledge of how anthropogenic activities affect soundscapes (Warren et al., 2006). Tropical forests, although rich in biodiversity and important for the provision of ecosystem services, are particularly understudied with regard to soundscapes (Scarpelli et al., 2020).

Landscape heterogeneity induces complex spatial and temporal acoustic partitioning, as species are non-randomly distributed along gradients of elevation (Caceres et al., 2011), slope (Nakashima et al., 2020), proximity to water (Rondinini et al., 2011), forest management type (Sollmann et al., 2017), roads (Stokes et al., 2010) and other human access points (Benítez-López et al., 2017). Sound also varies across time as species have variable activity patterns over the day and seasons (Depraetere et al., 2012; Haver et al., 2020; Vokurková et al., 2018). With changing seasons, the varying weather affects the sounds of the rain and the wind. Moreover, a changing moisture content also affects the overall acoustic properties of the environment, such as the reflectivity of wet versus dry surfaces and the distance that sound travels in relation to the denseness of the vegetation (Londhe et al., 2009). This variation makes soundscapes highly place and time specific, as each set of circumstances creates a unique spatio-temporal acoustic footprint (Fuller et al., 2015; Gasc et al., 2015; Lellouch et al., 2014). For soundscapes, these local effects are likely stronger than for other biomonitoring methods that target larger wildlife, e.g. walking line transects or camera trapping. This is because soundscapes also include smaller species like insects and amphibians, which respond more to localized heterogeneity. Given this influence of local variation on soundscapes, they can be used to detect subtle changes, enabling the tracking of biodiversity over time and space in changing landscapes. Conversely, the disadvantage is that a specific location and timing may exert a large influence on a soundscape, possibly complicating the interpretation of soundscapes (Sueur and Farina, 2015; Eldridge et al., 2016). For soundscape studies, this means that the heterogeneity in the landscape must be considered in the sampling design to prevent too much variation between the soundscapes of sampled sites. To account for this heterogeneity in the sampling design, it is important to understand how spatial and temporal variation affect soundscapes (Pijanowski et al., 2011).

Soundscapes include a wide variety of vocal animals, including birds, anurans, bats, primates, and several groups of insects (Ferreira et al., 2018). Acoustic indices reduce this diversity to a single value and for reliable ecological inference it is important to understand the relative contribution of different species groups to the soundscape (Fuller et al., 2015). Most acoustic diversity is driven by insects, due to their high abundance and their broad usage of both the time and frequency domains of the soundscape (Ferreira et al., 2018). While early soundscape research has primarily focused on birds, it has become evident that their contribution to acoustic diversity is relatively small compared to insects (Aide et al., 2017). Moreover, medium to large mammals have comparatively small bandwidths and short call durations. For the Neotropics it was found that these species contributed relatively little to soundscapes (Aide et al., 2017; Ferreira et al., 2018). Still, medium to large wildlife in Africa is comparatively more diverse and abundant than wildlife in other tropical forest regions and may therefore contribute differently to the soundscape. Studying which species contribute to the soundscape helps to understand which species can effectively be monitored with soundscapes. Species' contributions can be studied by corroborating species presence with other monitoring methods, such as camera trapping, at the sites where soundscapes are recorded.

A variety of acoustic indices for soundscape analysis are available (Buxton, McKenna, et al., 2018; Sueur et al., 2014; Towsey et al., 2014). One recently introduced index, soundscape saturation, is a promising, intuitive, and easy to understand proxy for acoustic diversity (Burivalova et al., 2018). Soundscape saturation is defined as the proportion of acoustically active frequency bins (i.e. arbitrary divisions of the frequency range) in a given minute of the spectrogram of a soundscape and calculates the degree of use of different acoustic bins. Soundscape saturation is based on the acoustic niche hypothesis, which states that species richness is strongly correlated with the total number of unique vocalizations (Krause, 1987), also referred to as 'sonotype' diversity (Ferreira et al., 2018). The reasoning driving this hypothesis is that time and frequency are resources over which vocalizing organisms compete to avoid acoustic interference. A species enhances its communication efficiency by occupying its own acoustic niche, thereby reducing overlap in time or frequency with other vocalizing species. As competition increases with increasing species richness, highly diverse systems see more acoustic niches filled. The total number of filled acoustic niches, measured as occupied frequency bins, can thus be used as a proxy for biodiversity which can be used for conservation management and translated into policy advice. As the index focuses on niche differentiation, it is particularly useful for species rich environments such as tropical forests (Burivalova et al., 2018; Burivalova, Purnomo, et al., 2019; Burivalova et al., 2021).

In this study, we aim to understand the spatial and temporal dynamics of soundscape saturation in the tropical forests of Gabon to establish which environmental, anthropogenic and temporal factors should be taken into account for future soundscape studies in Central Africa. Gabon harbors some of the most intact forests and richest communities of large wildlife in Central Africa (Abernethy et al., 2016), and is therefore a valuable study area for soundscape analyses, as future comparisons require baseline data of recorded soundscapes in relatively undisturbed sites. Gabon has an extensive logging industry that, although it is highly selective and its exploitation volumes are low (Karsenty, 2016), may affect acoustically active species (Burivalova et al., 2021). We sample various forest management types, including a FSC-certified logging concession, a non-certified logging concession, a multi-use forest which is used by local communities, abandoned and active slash and burn plantations, as well as a savanna area. We study the effect of distance to rivers, elevation, slope, distance to human access points, and signs of hunting on soundscape saturation. Furthermore, we compare saturation between the wet and the dry season. We then study how various management types affect saturation levels and calculate the dissimilarity of the soundscapes of the various land-use types. Last, given the rich forest wildlife of Gabon, we link acoustic data to camera trap data to study the relative contributions of the medium to large sized wildlife community to the soundscape.

2. Methods

2.1 Study area

We recorded the soundscapes of a mosaic of forest management types in Ngounie province, southwestern Gabon in November 2019 and January 2020 (Table 1). These forests are characterized as coastal dense evergreen tropical forests dominated by *Aucoumea klaineana* and *Sacoglottis gabonensis* (Caballé, 1978). Mean annual precipitation in the region is 1776 mm (Takenoshita & Yamagiwa, 2008). There are four seasons: a short dry season (January - February), a short rainy season (March - April), a long dry season (May – September), and a long rainy season (October – December). Most of the region, including what is now Moukalaba-Doudou National Park, has been selectively logged between 1962 and 1988 (Van Vliet & Nasi, 2008). In Gabon, logging cycles are 25 years and logging intensity is low compared to other tropical regions, with timber extraction volumes of ~4-8 m^3 per hectare (Karsenty, 2016). These forests are of high conservation value and retain high densities of critically endangered species such as western gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), and approximately 10% of the African forest elephant (*Loxodonta cyclotis*) population worldwide (Maisels et al., 2013; Strindberg et al., 2018; Takenoshita & Yamagiwa, 2008).

2.2 Study sites

We sampled two logging concessions near the medium-sized town of Mandji which has approximately 3000 inhabitants, as well as a variety of land-use types around the town itself. In *concession 1*, which became FSC-certified in 2009, hunting is banned and prevented by manned road barriers, guard patrols, and obstructing access to unused logging roads. In *concession 2*, which is conventionally logged, hunting is officially prohibited but this is not strictly enforced. We did not quantify forest structure or other forest characteristics for the two concessions, and therefore are not able to link differences in soundscapes to specific causal determinants. Nonetheless, regional timber extraction volumes are low (Karsenty, 2016) in certified and non-certified concessions. We therefore feel safe to assume that differences due to forest certification mainly manifest themselves by decreased hunting levels rather than changes in forest structure. In addition to the logging concessions we recorded the soundscapes of four different land-uses: 1) a segment of *multi-use forest* where artisanal logging and hunting is allowed throughout most of the year and restrictions are not strongly enforced during the non-hunting season; 2) *currently utilized rotational subsistence* plantations at the edges of the town; 3) *abandoned and overgrown subsistence plantations* found between the currently utilized plantations; and 4) a *savanna* area near the town where forest encroachment is prevented by annual burning to allow for mushroom gathering (Table 1).

Table 1. An overview of the sampled sites, the number of Acoustic Recording Units (ARU) and camera traps placed at each site, the number of ARUs yielding at least 90% and 80% of daily recorded minutes after malfunction and rain removal, mean number of recording days per ARU and season. Superscripts indicate which sites were included in each analysis: 1 = Seasonality, 2 = Landscape heterogeneity, 3 = Forest management type, 4 = Comparison with camera traps, 5 = Land-use type.

Site	Number of ARUs	Number of ARUs yielding at least 90% of daily recorded minutes after malfunction and rain removal	Number of ARUs yielding at least 80% of daily recorded minutes after malfunction and rain removal	Mean recording days/ARU	Season
Concession 1 FSC-certified ^{1,4}	14 (+ 36 camera traps)	12	12	5.0	Long rainy season
Concession 2 Non-certified ^{1,4}	36 (+ 36 camera traps)	32	32	3.8	Long rainy season
Concession 1 FSC-certified ^{1,2,3,5}	44	39	41	4.0	Short dry season
Concession 2 Non-certified ^{1,2,3,5}	34	27	28	3.5	Short dry season
Multi-use forest ^{2,3,5}	18	15	15	4.1	Short dry season
Occupied subsistence (slash and burn) plantations ^{5}	4	3	3	4.9	Short dry season
Abandoned subsistence (slash and burn) plantations ^{5}	2	2	2	4.5	Short dry season
Savanna ^{5}	8	3	5	4.1	Short dry season

2.3 Data acquisition

Data were collected over two separate periods: in the long rainy season (November 2019); and the short dry season (January 2020), using AudioMoth Autonomous Recording Units (ARUs) (Hill et al., 2019) and camera traps (Bushnell Trophy Cam HD, Model 119876). In the long rainy season, we installed 14 ARUs and 36 camera traps in concession 1 and 36 ARUs with 36 camera traps in concession 2 (Table 1). The large difference in number of recorders between sites was partly caused by a high number of recorder failures and partly by a programming mistake which was only encountered upon recovery of the ARUs. In the short dry season, we set up 44 ARUs in concession 1 and 34 ARUs in concession 2, and 18 in the multi-use forest. We furthermore installed several recorders in non-forested sites including occupied (n = 4) and abandoned (n = 2) plantations, and the savanna (n = 8). Exact installation locations were chosen randomly following a predefined systematic grid pattern with a 1 km spacing. The detection distance of sounds depends on the loudness with which a signal is produced. However, with one ARU per km2, it is unlikely that sounds are loud enough to be detected by multiple ARUs. ARUs were placed at breast height on trees and on one-meter-tall poles in the savanna area. Each ARU was placed in two ziploc bags to protect the device against rain. Devices recorded 1-min segments continuously at 48 kHz and 30.6 dB gain until battery power ran out, yielding 1.06-7.25 (mean: 4.40) recording days per ARU. All ARUs were programmed to start recording simultaneously. Camera traps were placed on the same trees with ARUs at a height of 30 to 45 cm and were required to have at least 4 meters of unimpeded view and were operational for approximately two months.

2.4 Sound data processing

Segments that were corrupted due to recorder failure were removed. To improve processing speed and to conform to other studies (Burivalova et al., 2018; Burivalova, Purnomo, et al., 2019), we down-sampled each 1-min segment to 22,050 Hz, as only few taxa vocalize above these frequencies. We excluded the 1-min segments whose maximum amplitude matched the amplitude limit of the recorder, as this was associated with either objects falling on the microphone or signal distortion caused by a cicada vocalizing on a tree too close to the recorder. Segments containing rain were classified using a threshold-based machine learning approach (Brown et al., 2019) and removed. To set the threshold, we manually annotated 650 files based on rain presence or absence and applied an MLP classifier with no MMSE STSA, all features, Relu activation, Adam solver, 50 iterations maximum, and no preprocessing (Brown et al., 2019). To each 1-min segment, the algorithm assigned a value between 0 and 1 indicating the probability that it contained rain. Segments with a classification threshold of 0.33 or higher were removed to produce a type-I error rate of 0.02. Together, the amplitude and rain filters removed 15% of the recorded segments. The remaining 1-min segments were converted to spectrograms using a short-time Fourier transform with a non-overlapping window of 512 samples. This divided each soundscape into 256 discrete frequency bins, each spanning approximately 43.0 Hz. The bin size is determined by dividing the Nyquist frequency (i.e. the maximum frequency beyond which aliasing will occur when transforming a sound signal into a spectrogram) of the signal (11,025 Hz) by the number of frequency bins.

2.5 Camera trap data processing

Species and number of individuals were manually identified from camera trap images. Photos taken more than ten minutes apart were considered to depict unique individuals. We calculated the relative abundance for each species as the number of unique individuals divided by the number of camera days. Species were then categorized into eight different animal guilds: apes, birds, carnivores, elephants, monkeys, pangolins, rodents, and ungulates. The relative abundance index (RAI) of each guild at each camera trap was calculated as the mean RAI of its affiliated species.

2.6 Soundscape saturation

We calculated soundscape saturation following Burivalova et al. (2018) for each 1-min segment and took the average value for each minute in the 24-hour cycle across the multiple recording days, producing 1440 saturation values per ARU. ARUs that missed more than 10% of minutes due to malfunctions and rain (n = 27) were excluded from all analyses. For the soundscape dissimilarity comparison between the land-use types we included ARUs that missed up to 20% of the minutes of the day, to retain sufficient data points for the savanna recordings (Table 1). The remaining missing values were estimated as the average of the two adjacent minutes. All soundscape saturation code was written in R (R Core Team, 2020) and can be found in the Supplementary Information. We first studied whether the length of our recording period of five days was sufficiently long to capture the major acoustic variability, by plotting the range of soundscape saturation values of ARUs with recording periods of 2, 3, 4 and 5 days (n = 9). Ranges were plotted for eight different sets of randomly combined ARUs to ensure that the findings are consistent despite the small sample size. Next, to quantify the ability of soundscape saturation to predict biodiversity, we inspected the spectrograms of two randomly chosen sets of 100 consecutive minutes and counted the total number of sonotypes (unique vocalizations) for each minute. Some minutes experienced signal distortion due to a cicada too close to the device (24 of the 200 selected minutes) and were removed by the amplitude filter without replacement from other recordings. The first 100-minute segment began at 5 AM and the second at 5 PM. We opted for the annotation of longer consecutive 100-minute segments over randomly chosen 1-minute segments, because it allowed us to review sonotypes from start to end. Recognizing partially overlapping sonotypes thereby becomes easier and arbitrarily splitting sonotypes over multiple 1-minute segments is prevented. Verification was performed blindly, i.e. the person annotating did not know the metadata of the recording. The unique number of sonotypes was then cross-referenced with soundscape saturation by using a Pearson's correlation test to measure whether saturation correlated with the observed richness of the vocalizing fauna.

2.7 Statistical analyses

We first evaluated soundscape saturation in relation to the following covariates: elevation, distance to the nearest river, human accessibility defined as the shortest distance to a point of access with a car or canoe, hunting intensity, management/ land-use type, latitude, longitude, and slope (Table 2). The relative contribution of these covariates to soundscape saturation was estimated using Aikake's Information Criterion for adjusted sample size (AICc), which allowed us to select the combination of covariates that best explain the variation in soundscape saturation. Our study area contained a gradient of increasing elevation and distance to the nearest river from northwest to southeast. As a result, latitude and longitude masked a lot of the variation which we thought was better attributed to elevation and river proximity. We therefore excluded latitude and longitude from model selection, as done in other studies (Poulsen et al., 2011). Each minute of the 24-cycle was fitted separately, as acoustic activity naturally fluctuates throughout the day-night cycle. This produces the combination of covariates that best explain the variation in acoustic species richness for each minute of the day. The best models throughout the entire day are those that perform best for the most minutes of the 24-hour cycle (Burivalova et al., 2018).

To more closely investigate covariates relating to human impact, we compared soundscape saturation across three sites differing in the type of management (i.e. FSC-certified logging, non-certified logging, and multi-use forest). We did not include the plantations and savanna recordings, because those sites are vastly different, non-forested ecosystems, which renders their acoustic diversity incomparable. As differences between forest management types were expected to be subtle, the comparisons for this analysis were made during dawn (05:00-06:00) and dusk (18:00-19:00) choruses, as these moments contain the highest acoustic activity and are therefore most likely to show differences in soundscape saturation following the acoustic niche hypothesis. The sample size differed between sites, which complicates drawing conclusions about whether the sites differ in soundscape saturation levels, or whether a potential difference is merely the result of a differential sampling size. We therefore compared the forested sites in two analogous analyses. In the first, we used all data available to decrease variation and increase statistical power. However, to confirm whether the same effect can be found with an equal sample size between the sites, we also did the same analysis using a randomly picked set of ARUs with an equal number per forest management type (n = 6). The latter analysis has a small sample size and therefore less statistical power. The analysis was therefore repeated eight times, each with a new random combination of ARUs to verify whether the outcomes are consistently similar to the analysis with all the available data. Subsequently, to compare soundscape saturation sampled in both seasons, we used a paired-sample t-test of the locations that were recorded in both seasons (n = 22). The number of paired ARUs is lower than the overall number of ARUs installed in the rainy season because we did not resample all rainy season locations in order to capture more heterogeneity in the landscape in the dry season.

With large differences in ecosystems, species communities are less similar, which makes comparing soundscape saturation less useful as a proxy for biodiversity. We therefore also used another related index, the soundscape dissimilarity index (S_d) (Burivalova, Purnomo, et al., 2019), to compare the acoustic communities of all the recorded land-use types by ordinating all ARUs using non-metric multidimensional scaling (NMDS). This index characterizes each frequency bin of a 60 s soundscape as

Table 2. A description of the covariates of spatial variation used in this study.

Covariate	Description	Range or categories
Slope	Estimated slope at ARU in the field	0-5°, 5-20°, or > 20
Distance to river	Shortest Euclidean distance to a river (m)	Range 31-4876 m, mean 1890 m
Hunting	Wire snares, shell cases, and/or hunting camps found within 500 m of a ARU	Presence / absence
Human accessibility	Shortest Euclidean distance to either a road with vehicle access or a navigable river	Range 18-15475 m, mean 8040 m
Elevation	Elevation above sea level (m)	Range 38-417 m, mean 200 m
Management/ land-use type	Type of ecosystem.	FSC-certified logging, non-certified logging, multi-use forest, occupied subsistence plantations, abandoned subsistence plantations, savanna

the maximum decibel value minus the background noise creating a daily soundscape grid of 1440 minutes by 256 frequency bins. Following Burivalova, Purnomo et al. (2019), we split this grid into 192 non-overlapping segments of 32 frequency bins by 60 minutes. Each segment is in turn divided into subsegments of 8 bins by 10 minutes, each overlapping its neighboring subsegments by 4 bins and 5 minutes. Each soundscape is thus composed of 192 x 77 values. For two sites, the absolute difference of each corresponding subsegment pair is calculated. The mean of all these pairwise differences produces the final value for S_d between two sites.

Finally, we performed a second AICc model selection using only the locations where camera traps were placed together with acoustic recorders by using the RAI of the eight selected animal guilds as covariates to compare soundscape saturation with camera trap data and to investigate the relative species' contributions and the degree of overlap between the two monitoring techniques. Interactions were not fitted due to the small sample size.

3. Results

3.1 Recording length and verification of soundscape saturation

We first examined whether our five-day recording period was sufficiently long by plotting the range of soundscape saturation values for ARUs that recorded various lengths (Figure S1). This showed that the range of saturation values did not increase after three to four days (Kruskal-Wallis chi-squared = 7.4961, df = 3, p-value = 0.05766), indicating that five days of recordings were sufficient to capture the majority of short-term acoustic variability. To verify whether soundscape saturation is a true proxy for biodiversity, we tested whether its estimate of acoustic diversity corresponded to the number of unique vocalizations on an annotated subset of soundscapes and found that this was indeed the case (P < 2.5e-08, R = 0.40; Figure S2). No occurrences of anthrophony were observed.

3.2 Landscape heterogeneity

To investigate the effect of covariates on soundscape saturation, we used AICc model selection for all ARUs that were installed in the forest (Table S1). This revealed three models that were dominant during more than 10% of the day: the null model (13.1%), the model only including human accessibility mostly during the nighttime (11.3%), and the model including human accessibility and distance to the nearest river (10.8%) (Figure 1 and S3). Thus, shorter distances to the river and human access points correlated positively to soundscape saturation and were by far the most important covariates. Throughout the day, the total amount of dominance per covariate was 28.5%, 22.4%, 18.6%, 15.6% and 14.9% for human accessibility, river proximity, elevation, slope and hunting, respectively.

3.3 Forest management type

The mean soundscape saturation values of the three differently managed forests; FSC-certified, non-certified and a multi-use forest, were not significantly different during the dawn chorus (one-way ANOVA; F = 1.23, P = 0.30), but they differed during the dusk chorus (one-way ANOVA; F = 8.27, P = 5.53e-04). Post-hoc comparisons with a Tukey HSD test revealed that the multi-use forest differed significantly from the FSC certified (P < 0.001) and non-FSC certified (P = 0.045) logging concessions during

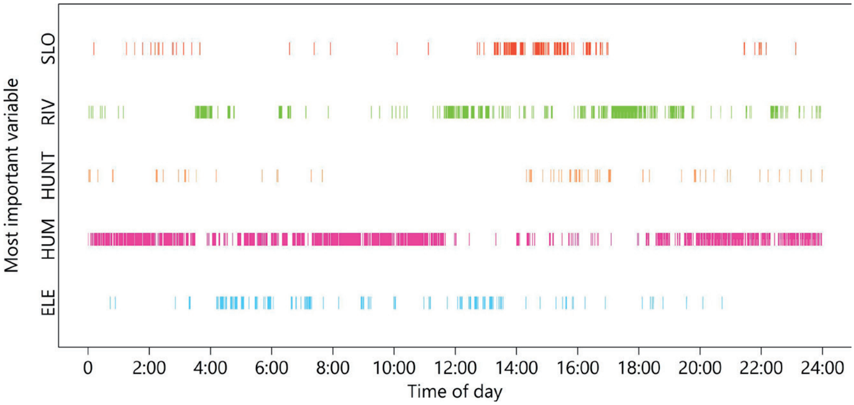

Figure 1. The relative importance of spatial landscape gradients in explaining soundscape saturation throughout the 24-hour cycle. Each variable is colored when it the most relevant variable for explaining the soundscape saturation for a given minute of the day. Covariate abbreviations: SLO, slope; RIV, distance to nearest river; HUNT, presence/absence of signs of hunting; HUM, distance to either nearest human settlement or point of vehicle access; and ELE, elevation.

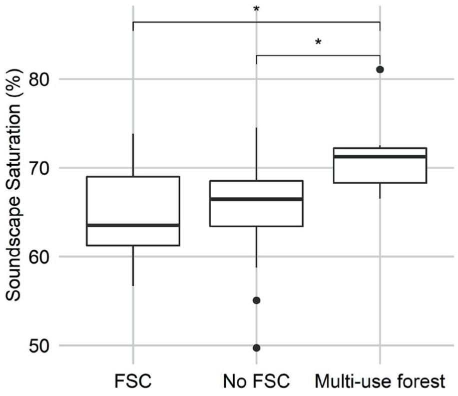

Figure 2. Mean soundscape saturation during the dusk chorus in two logging concessions (FSC (n = 19_and non-certified (n = 27)) and a multi-use forest (n = 6). We excluded ARUs that were further than 2500 meters away from a river because these were almost exclusively found in the FSC-certified concession. * = P < 0.05.

the dusk chorus. However, the covariate analyses indicated the importance of river proximity, and ARUs in the FSC-certified concession were on average much further away from rivers (mean = 2647 m), compared to those in the non-certified (mean = 1145 m) and multi-use forest (mean = 2573). We therefore decided to exclude all ARUs (n = 29) more than 2500 meters away from a principal river. Again, acoustic diversity at dusk differed significantly between the multi-use forest (n = 6) and the FSC-certified (n = 19, P = 0.018) and the non-certified (n = 27, P = 0.022) logging concessions (F = 4.36, p = 0.018; Figure 2 and S4). Also with small sample sizes (n = 6), a consistently similar pattern was found when the same analysis was performed eight times with randomly picked equal sample sizes between management types (Figure S5). It should be noted that although human accessibility also was a dominant covariate, we did not discard any recordings based on this variable because it would result in removing the complete multi-use forest recordings as this forest was more closely situated to the town than the forest concession.

3.4 Seasonality

We used the combined data of the FSC and non-certified sites to study seasonal fluctuations in acoustic diversity between the long rainy season of 2019 and the short dry season of 2020. A pairwise comparison between sites in both seasons revealed that the rainy season exhibited significantly more acoustic diversity than the short dry season (t = 3.16, P < 0.0048; Figure 3 and S6).

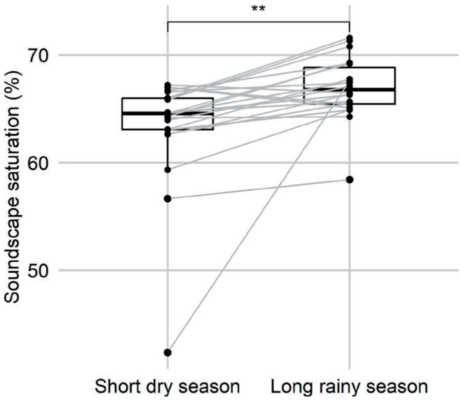

Figure 3. Seasonal changes in soundscape saturation of the combined data of the FSC and non-certified sites. ** = P < 0.01.

3.5 Land-use type

Using the acoustic dissimilarity index S_d (Burivalova, Purnomo, et al., 2019), we characterized the soundscape of each ARU to compare differences in acoustic activity between the recorded land-use types (Table 1; Figure 4 and S7). The axes of figure 4 were chosen arbitrarily to best represent the dissimilarity of the ARUs. Based on this ordination, the soundscapes of the land-use types can be placed into three distinct groups: savanna, active subsistence plantations, and forested land-use types, which included both types of logging concessions, the multi-use forest, and the abandoned subsistence plantations.

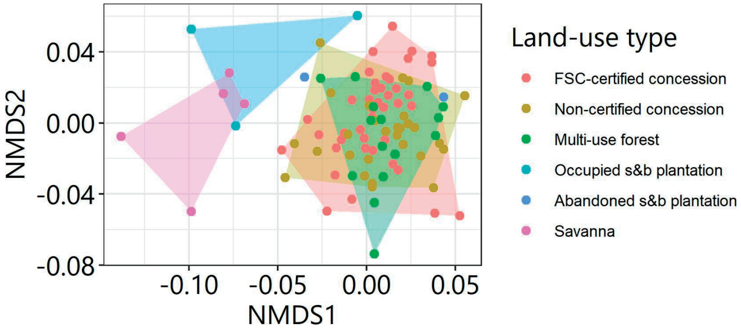

Figure 4. NMDS ordination of the soundscapes recorded in various land-use types, using the soundscape dissimilarity index. Colored shapes indicate convex hulls. FSC certified logging concession (n = 41), non-certified logging concession (n = 28), multi-use forest (n = 15), occupied slash and burn plantation (n = 3), abandoned slash and burn plantation (n = 2) and savanna (n = 5).

3.6 Comparison with camera trap data

We performed a second AICc model selection using only the soundscape saturation values of ARUs that were placed together with camera traps and with the RAI of the eight animal guilds as covariates (Table S1; Table S2). In this case, the null model without any of the species' covariates was the best fit during 31% of the 24-hour period (Figure S8 and S9). The second-best performing model (21%) included the mean RAI of the great apes (i.e. *G. gorilla* and *P. troglodytes*), which was also the most important covariate across all models. The relative contribution of the bird guild RAI was low throughout most of the day but peaked during the dusk chorus.

4. Discussion

Here we report the first soundscape saturation analyses (Burivalova et al., 2018) of African tropical forests, to assess acoustic diversity in relation to environmental, anthropogenic, and temporal heterogeneity. The most important covariates contributing to soundscape saturation were proximity to rivers and human accessibility, which were both associated with higher acoustic diversity. For the forest management types, we found no difference in soundscape saturation between the FSC-certified and non-certified forest, but found higher saturation in a multi-use forest. For the seasonal comparison, we found that acoustic diversity was higher during the rainy season than the dry season. Finally, using paired camera trap data, we did not find strong evidence that medium to large sized wildlife contributes significantly to soundscape saturation, highlighting the complementarity in species coverage between acoustical and visual monitoring and the benefits of a combined approach.

4.1 Landscape heterogeneity

Covariate analysis showed that shorter distances to human access points were positively correlated with soundscape saturation. The higher acoustic diversity in connection with human disturbance was unexpected and contrasts with studies that found less biodiversity closer to human access points, although these studies did not look at acoustic diversity (Benítez-López et al., 2017; Lhoest et al., 2020). It is unlikely that anthropogenic noise itself contributed much to soundscape saturation, as distances to human access points were at least 1 km. It is important to note, however, that traffic noise can affect the spectral structure of the soundscape by masking sounds and subsequent adjustments of song type and frequency by vocalizing species (Oden et al., 2015). This correlation can however best be explained by trophic disruptions of the ecosystem (see below). Hunting did not prove to be a large contributor to soundscape saturation, which can be explained, as hunting mainly affects larger and generally less vocally active wildlife.

We found that proximity to rivers positively affected soundscape saturation. Soundscapes near to rivers are likely more diverse due to the increased anuran and insect diversity, which are positively correlated with microhabitat gradients in riparian systems (Campos-Cerqueira et al., 2019; Depraetere et al., 2012). Insects are likely to constitute a prominent component of soundscapes which explains the impact of distance to rivers found here (Aide et al., 2017; Diepstraten and Willie, 2021). Figure 1 showed that the relative variable importance of elevation is strongly correlated with distance to rivers, in line with rivers lying lower, which in turn explains the redundancy of elevation in the model selection. The same logic applies to slope, because it is also correlated with elevation. Moreover, there was only limited variation in elevation over our study sites (Table 2).

4.2 Forest management type

Contrary to our expectations but in line with Diepstraten and Willie (2021), we found that the more disturbed multi-use forest displayed higher acoustic diversity compared to the logging concessions, which is likely explained by several reasons. First, both forest-interior species and edge species may coexist in the multi-use forest, increasing overall species richness (O'Dea & Whittaker, 2007; Welford, 2000). This effect may be enhanced in this forest as birds may be attracted by the opportunity to forage on the subsistence plantations nearby (Poulsen et al., 2011). Second, insects may be attracted to the increased light availability in the more disturbed multi-use forest. Cicadas, start to vocalize when the sun hits them and are likely to contribute a lot to the soundscape. In areas with abundant light gaps (roadsides, multi-use forests, river banks), the sun may hit the cicadas earlier than within the closed canopy forest, prompting them to sing. Third, the multi-use forest likely suffers from the highest hunting pressure of the three management types as it is closest to the town, which likely depleted higher trophic levels. Cascading effects in the ecosystem, such as a loss of top-down control by predators, may result in a release of species that are otherwise suppressed and that vocalize more than the hunted species (Abernethy et al., 2013; Terborgh, 2015). Future studies are necessary to elucidate the meaning of high acoustic diversity. While the higher soundscape saturation of the multi-use forest might initially appear positive, it is in fact likely to indicate severe defaunation of larger, silent species not captured by acoustic methods and the subsequent release of more vocal, smaller species. Increasing soundscape saturation in human disturbed systems would in such cases still be in line with the acoustic niche hypothesis, but does not represent an ecologically desirable situation from a conservation perspective. Thus, using soundscape saturation as a proxy for biodiversity in a conservation setting does not simply require maximization of saturation, but necessitates a more context-dependent understanding of what creates differences in soundscape saturation. This implies that comparing saturation levels is only useful when ecosystems are structurally similar and consist of comparable species communities. Examples include a comparison of forest management types in logged forests, or comparing oil palm plantations with and without pesticides, but does not include comparing a logged forest with an oil palm plantation.

We found no differences in soundscape saturation between the FSC-certified and non-certified sites. The most likely explanation for this is that soundscape saturation may not be the right method to gauge the environmental impacts from forest certification. That is, soundscape saturation is a measure of acoustic diversity, not of abundance. If an ecosystem is impoverished in species abundance, but not in species diversity, this is unlikely to be captured by soundscape saturation. Extraction volumes of logs in Central Africa, and therefore the overall environmental impact, are low compared to other tropical regions (Karsenty, 2016). Thus, if a site has not lost any species, the differences between two types of forest management may be too subtle to distinguish with soundscape saturation. Moreover, the most likely differences between the two types of forest management are potentially going undetected as larger species, that are expected to gain most from the protection of FSC's stricter hunting regulations, are generally less vocal (Ferreira et al., 2018). So even though our camera trap data indeed shows that the FSC-certified site boasts a higher abundance of wildlife (Table S2), this is not expressed in a significantly different level of soundscape saturation.

To correct for the influence of distance to rivers between the forest management types, we excluded sites with a distance larger than 2500 meter from a river from the analyses. Even though human accessibility also had a high relative importance for saturation levels, we did not exclude recordings based on this covariate. Namely, sites with high human accessibility were heavily skewed to the multi-use forest and their exclusion would result in excluding the multi-use forest entirely. Thus, in this specific case the skewed anthropogenic covariate between various land-use types was of little consequence because the nature of the compared sites themselves implies that anthropogenic covariates are unevenly distributed. This would not be the case when soundscape saturation is compared within one management type and all other variables that may impact the soundscape should be roughly kept equal. The significance of the influence of covariates is thus context dependent.

4.3 Seasonality

Soundscape saturation was higher in the long rainy season of 2019 than in the short dry season of 2020, which contrasts earlier findings by Burivalova et al., (2021). The increased vocal activity in our rainy season recordings is likely caused by increased insect (mainly cicadas) and anuran activity during the rainy season (Galoyan et al., 2017; Rodriguez et al., 2014). Primates are also known to be far noisier in the wet season. They can afford to be more active because more food is available (Poulsen et al., 2001). In the dry season, primates move little to conserve energy when food is less abundant. Finally, the physical properties of the forest, e.g. the reflectance which causes sound to travel farther, also change during the rainy season. Given the site-specific seasonal variation, it is paramount that future soundscape studies take the timing of recordings into account when comparing sites. Although it is often logistically difficult to install recorders at various sites simultaneously, care should be taken to avoid large gaps in time between different sites of interest. It will also be valuable to record for longer time periods to capture more temporal variation, which will aid in understanding cyclical soundscape patterns or impacts of events undetectable by this short-term study (Burivalova et al., 2021). To achieve the necessary battery power, recordings could be made only at the most ecologically relevant times, such as the dusk chorus. During this time the soundscape saturation was the highest in our data and competition for time-frequency niches is likely the most severe. Furthermore, it is important to report how rain is dealt with in the analyses in detail, as the number of recordings that are retained that contain rain, directly affect the index that is calculated over a soundscape.

4.4 Land-use type

We used the soundscape dissimilarity index (S_d), to characterize and compare the soundscapes of all our recorded land-use types (Figure 4). The savanna and active subsistence plantations formed two distinct groups, although the sample sizes are too small to establish statistically significant differences as was done for land-use types in an oil palm landscape in Colombia (Furumo & Mitchell Aide, 2019). Despite of the lack of replication and therefore statistical power, we chose to analyze the active and abandoned subsistence plots separately in the dissimilarity analysis. This was done because the active subsistence plots clearly display dissimilarity from the forested sites, while the abandoned subsistence plots show greater acoustic similarity to the forested sites. This similarity nicely illustrates how soundscapes of abandoned subsistence plots quickly revert to their original acoustic state. These findings also indicate that soundscape dissimilarity can be a highly suitable method for tracking coarse-scale acoustic changes in the landscape, which can potentially be applied in monitoring and quantifying the biodiversity of reforestation efforts, or in quantifying recovery of degraded or fragmented forests.

There was little dissimilarity between the soundscapes recorded in the two logging concessions, the multi-use forest, and the abandoned subsistence plantations. Note that this does not immediately imply that soundscape saturation levels between these land-use types are equal, as the structure of the soundscape can be largely similar in terms of which time-frequency segments are filled resulting in high similarity, even when acoustic diversity differs strongly. Soundscape dissimilarity is a coarser index than soundscape saturation and is more informative for detecting larger differences between acoustic communities. This merits further research into which land-use changes can effectively be monitored and quantified either using soundscape saturation or soundscape dissimilarity. Future studies can use a combined approach to address how soundscape saturation and dissimilarity changes over a temporal gradient of slash and burn subsistence plots to shed light on the acoustic recovery of soundscapes of this dominant land-use type in tropical Africa (Nasi et al., 2012).

4.5 Comparison to camera trap data

We found very little evidence for a correlation between the relative abundance of wildlife guilds as observed by camera traps and soundscape saturation, except for some evidence for the contribution of great apes (Table S1). The relative contribution of great apes was highest during the night when apes are predominantly inactive (Figure S8 and S9). This finding suggests that the correlation between ape abundance and soundscape saturation was not caused directly by their sounds contributing to soundscapes. A plausible explanation is that the habitat preference of these species is related to acoustic diversity through environmental conditions such as vegetation structure or distance to water. Our results thus seem to corroborate that medium to large forest wildlife, mostly mammals, provides a relatively small contribution to the soundscape of African tropical forests (Diepstraten and Willie, 2021), as was previously also found for the neotropics (Aide et al., 2017; Ferreira et al., 2018). It is important to note, however, that camera traps are not very suitable for observing birds, limiting our ability to draw conclusions about their contribution to the soundscape. Moreover, our camera traps were in the field for a much longer period (approximately two months) than the ARUs (five days). The difference in deployment period is linked to the ability of the two devices to detect animals. On the one hand, collecting camera trap data over only five days would not be useful, as cameras only have a very small spatial observation window which needs to be compensated with a longer observation period to capture a representative image of the wildlife community. ARUs, on the other hand, can capture sounds from larger distances, and thus require less time to capture diversity. Yet, it is not sure whether large animals with large home ranges were present in the area around the ARU in the five days of the recording, even though they might have been observed multiple times on the camera in the subsequent two months.

4.6 Outlook

We studied how soundscape saturation is affected by land-use/management type, environmental heterogeneity, seasonality, and how saturation correlated to camera trap data. Regional soundscape explorations are required to understand how spatio-temporal variation is reflected in soundscapes and to provide guidance for future studies for which factors should be controlled in relation to installation locations (Burivalova, Game, et al., 2019). Soundscape saturation has presently only been applied in the tropical forests of Papua New Guinea and Indonesian Borneo (Burivalova et al., 2018; Burivalova, Purnomo, et al., 2019; Burivalova et al., 2021). We answer the call to focus acoustic research on terrestrial, tropical wildlife, and how it is affected by human pressures (Scarpelli et al., 2020). We showed that soundscape saturation can be effectively used to track and quantify vocally active species across various types of forest management with potential applications for biodiversity monitoring in reforestation, rehabilitation, or degradation settings. We also showed that not all species can be effectively monitored using this method and that soundscape saturation requires a context-dependent interpretation of species' contributions and of the importance of spatial and temporal variation. Overall, given that spatiotemporal variation is carefully considered, soundscape saturation may be highly suitable for tracking vocal biodiversity through time and space. Spatiotemporal variation implies that to compare soundscapes, all factors affecting a soundscape need to be identified. They then either need to be standardized across the sampling units, or controlled during the analysis.

The field of eco-acoustics is still developing, with many promising avenues for future research. With our study, we highlight the opportunities and challenges of soundscape saturation studies. Opportunities include the potential to monitor landscape level changes in biodiversity, and the complementarity of species coverage to other monitoring methods. Challenges include correctly dealing with landscape heterogeneity and increasing our understanding which species make up the soundscape. Both soundscape saturation and soundscape dissimilarity can be used to discern changes within and between land-use types. Having an effective way of quantifying landscape level quality and changes in biodiversity can be an important asset for the implementation of verifiable controls for conservation efforts. Considering the large quantity of acoustic indices (Buxton, McKenna, et al., 2018), much remains to be learned about which indices are most relevant for particular land-use types, ecosystems, and species representations. Which species group contributes also depends on the acoustic index (Ferreira et al., 2018; Fuller et al., 2015; Gasc et al., 2015) and although generalizing metrics like soundscape saturation can serve as proxies for vocal biodiversity in general, they do not represent all species equally well. The most vulnerable species, those with large body sizes, require other monitoring methods to inform conservation actions (e.g. Zwerts et al., 2021). Combined approaches of acoustic monitoring with camera trapping are desirable, as both methods share similar logistical benefits, while being complementary in species coverage (Buxton, Lendrum, et al., 2018).

The difficulty in connecting soundscape indices to species groups does not negate their usefulness given their efficacy in monitoring overall ecosystem structure and stability. Any form of disturbance that affects biodiversity will likely also have an impact on the soundscape and can thus be measured and quantified. Elucidating species' contributions is an important part of future soundscape work. One approach to disentangle the relative importance of taxonomic groups in the soundscape, may be to identify the frequency ranges and activity patterns characteristic to different groups of interest and use this as a basis for classification, as has been done to distinguish biophony from anthrophony (Kasten et al., 2012). Insight derived from such studies may help to further elucidate species' contributions. Soundscape research is still new and looking ahead we see much value in studies addressing species' contributions in a range of land-use types to strengthen our understanding of how soundscapes relate to biodiversity.

Acknowledgements

We are grateful to the logging companies for access to their concessions and for their logistical support. The work was carried out with permission from the Centre National de la Recherche Scientifique et Technologique (CENAREST) under research permit n°AV AR0046/18. This study was supported by funding from the graduate programme 'Nature Conservation, Management and Restoration' of the Dutch Research Council (NWO), the 'Programme de Promotion de l'Exploitation Certifiée des Forêts' (PPECF) de la COMIFAC (à travers la KfW), and WWF the Netherlands. We thank Kathryn Barry for proofreading our manuscript.

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Supplementary materials

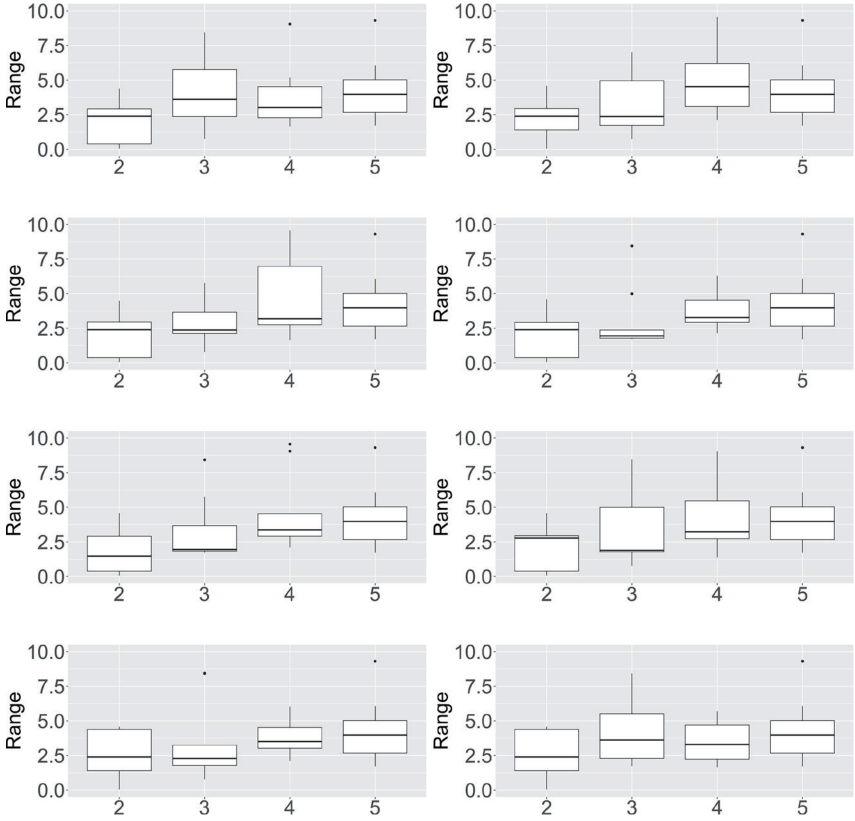

Figure S1. The range of soundscape saturation (SS) values for ARUs that recorded periods of 2, 3, 4 and 5 days (n = 9). The ranges were plotted for eight different sets of randomly combined ARUs.

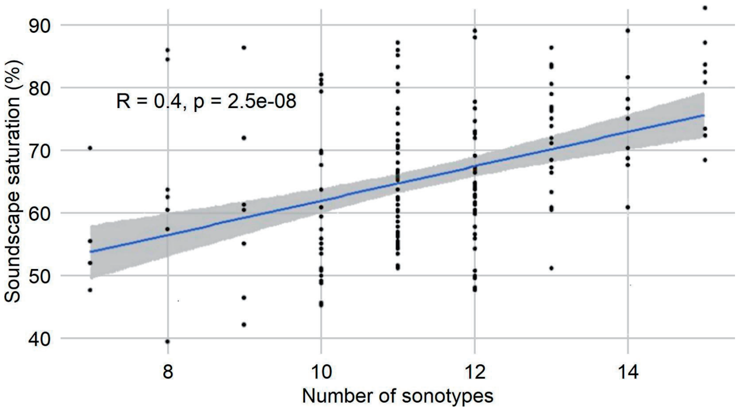

Figure S2. A positive correlation between soundscape saturation and unique vocalizations (sonotypes), indicating the predictive ability of soundscape saturation as a proxy for biodiversity.

Table S1. The covariates included in the models that performed best for more than 10% of the day in the AICc model selection analyses.

	Covariates included	% Of day the best model
All forested sites		
1	None	13.1
2	Human accessibility	11.3
3	Human accessibility + Distance to river	10.8
Camera trap ARUs only		
1	None	31.3
2	Relative abundance of apes	21.4

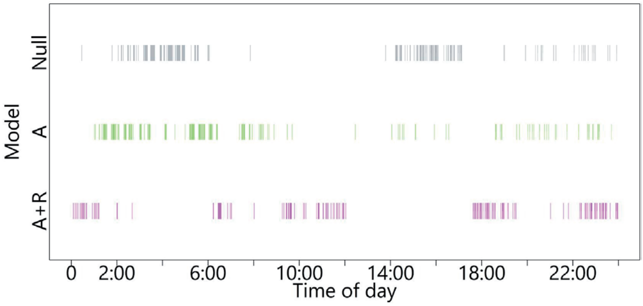

Figure S3. The models explaining soundscape saturation in the forested sites that performed best for more than 10% of the day throughout the 24-hour cycle. Covariate abbreviations: Null, null model; A, distance to either nearest human settlement or point of vehicle access; R, distance to nearest river.

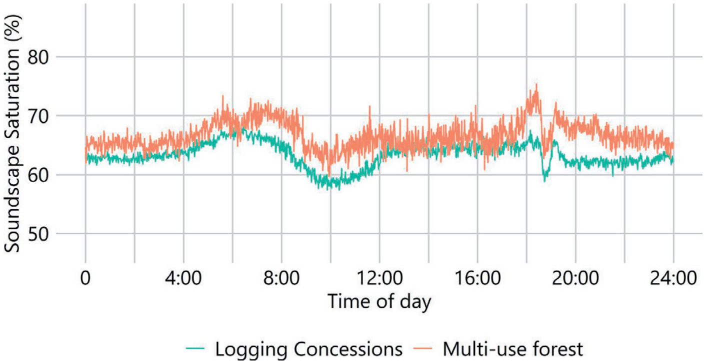

Figure S4. Differences in acoustic diversity, as measured by soundscape saturation, between the combined logging concessions (n = 46) and a multi-use forest (n = 6) during the 24-hour cycle in a Gabonese rainforest.

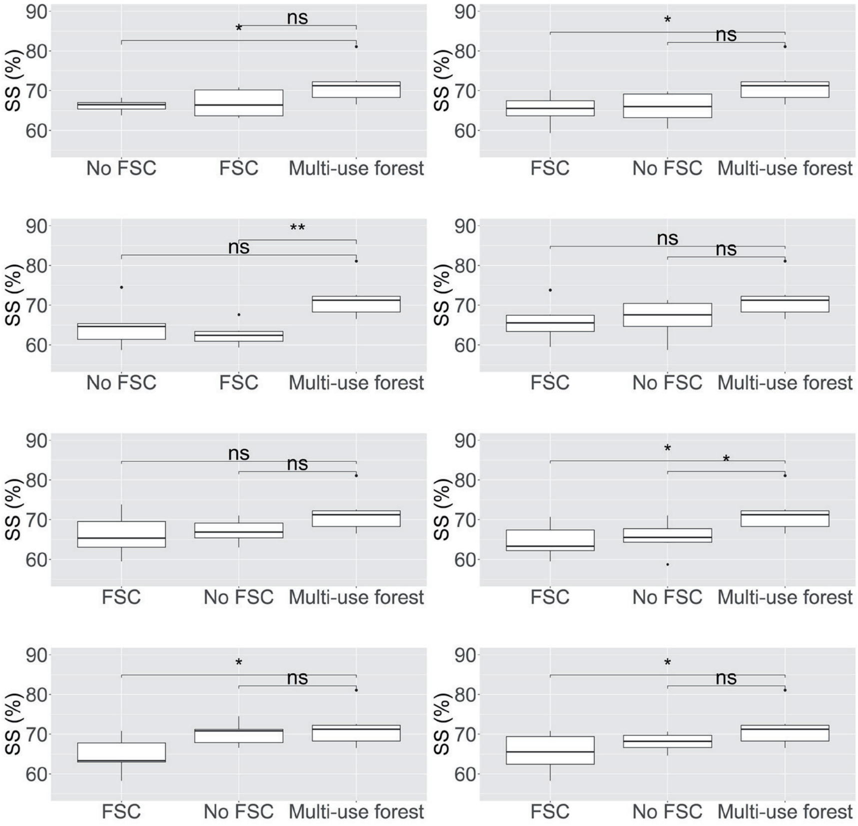

Figure S5. Mean soundscape saturation during the dusk chorus in two logging concessions (FSC and non-FSC-certified) and a multi-use forest. A Wilcoxon Rank Sum test was performed eight times, each with randomly picked equal sample sizes (n = 6) between management types. We excluded ARUs that were further than 2500 meters of a river because these were almost exclusively found in the FSC-certified concession. * = P < 0.05; ns = not significant.

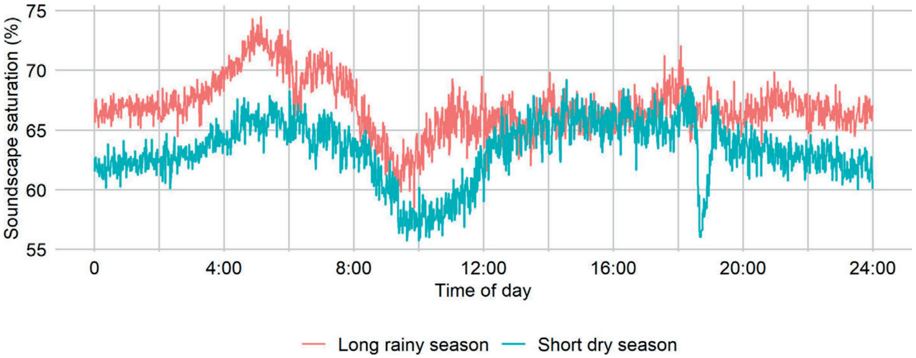

Figure S6. Seasonal changes in acoustic diversity, as measured by soundscape saturation, during the 24-hour cycle in a Gabonese rainforest.

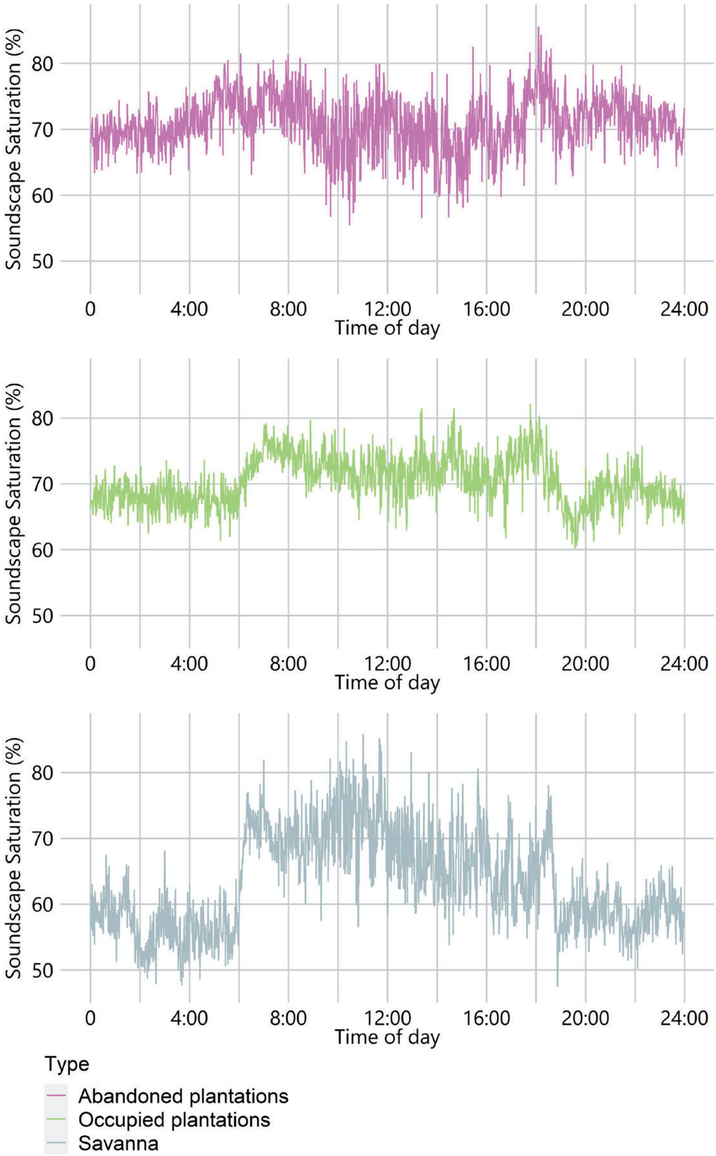

Figure S7. Differences in acoustic diversity, as measured by soundscape saturation (SS), for occupied (n = 4) and abandoned (n = 2) plantations, and a savanna (n = 8) during the 24-hour cycle in a Gabonese rainforest.

Table S2. Relative abundance (observations/camera trap day) of animal guilds for the FSC-certified and the non-certified logging concessions as captured by camera traps, expressed as average daily trap rate over all camera traps per site.

Site	Ape	Bird	Carnivore	Elephant	Monkey	Pangolin	Rodent	Ungulate
FSC-certified	0.026758	0.00836	0.005559	0.07922	0.008359	0.000939	0.043141	0.07242
Non-certified	0.005361	0.006067	0.006075	0.020334	0.003519	0.001947	0.042607	0.039375

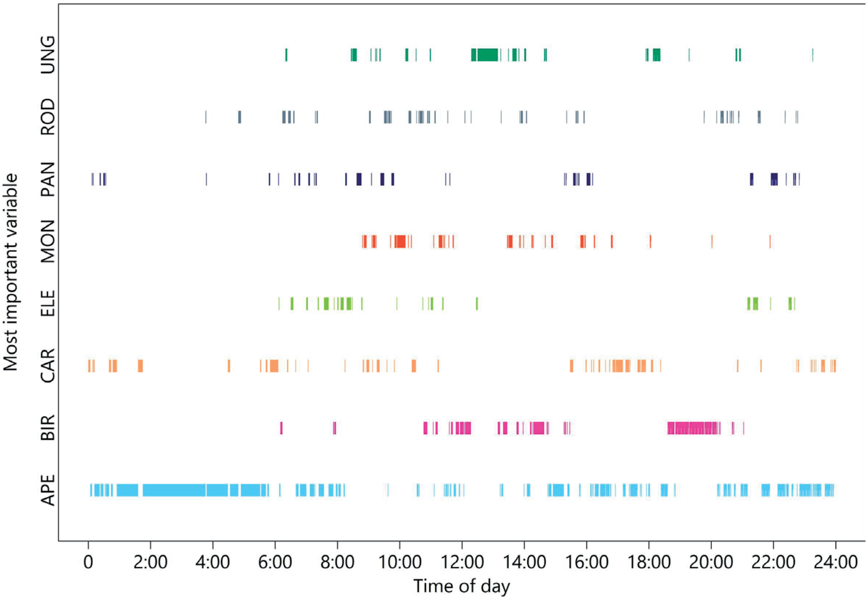

Figure S8. The relative importance of eight animal guilds in explaining soundscape saturation throughout the 24-hour cycle. Each variable is colored when it the most relevant variable for explaining the soundscape saturation for a given minute of the day. Covariate abbreviations: APE, great apes; BIR, birds; CAR, carnivores; ELE, elephants; MON, monkeys; PAN, pangolins; ROD, rodents; and UNG, ungulates.

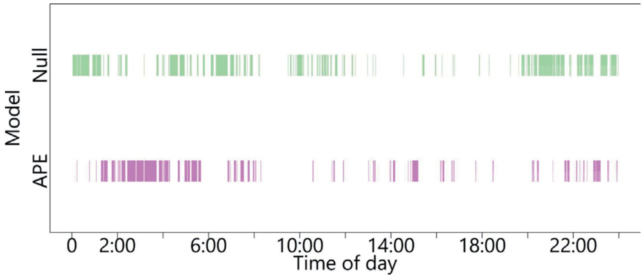

Figure S9. The models explaining soundscape saturation that performed best for more than 10% of the day, in relation to the wildlife observed by camera traps, throughout the 24-hour cycle. Covariate abbreviations: Null, null model; APE, great apes.

Chapter 6

Synthesis and general discussion

Overview

This research addressed wildlife conservation and monitoring in logged tropical forests. The general aims of this thesis were to assess whether wildlife is more effectively conserved in FSC-certified logging concessions than in non-FSC concessions, and to explore how wildlife populations can best be monitored in tropical forests.

Chapter 2 extensively reviewed three main monitoring methods used in tropical forests: human observations, camera traps, and passive acoustic sensors. This review, among others, highlights the need for monitoring to be done with clearly stated objectives, and in principle recommends combining different methods to attain an image of the wildlife community that is as complete as possible. Acoustic monitoring, however, still requires a high level of expertise and is not yet as accessible as using camera traps. This is mainly because of the difficulties related to automated detection, which is a prerequisite for acoustic monitoring. Based on our findings, camera trapping was found most cost-effective for a study on landscape scale as conducted in chapter 3.

Chapter 3 showed that wildlife was observed more frequently in FSC-certified forests than in non-FSC concessions. The effect was most pronounced for species weighing over 10 kg, and for species of high conservation priority such as the Critically Endangered forest elephant, large carnivores and primates. This study provides strong evidence that FSC certification benefits wildlife conservation and therefore we argue that FSC-certified forest management, or equivalently stringent schemes and controlling mechanisms, should become the norm for timber extraction, since inaction will result in half-empty forests dominated by rodents and other small species.

Chapter 4 presented a detection algorithm for several primate species which can effectively detect multiple primate species in acoustic recordings. Training robust classifiers requires sizeable, annotated datasets, for which data cannot easily be recorded in the wild. To circumvent this problem, we recorded four primate species under semi-natural conditions in a wildlife sanctuary in Cameroon. We also present a method to efficiently select relevant audio segments in recordings, which can be used to collect training data for the training of detection algorithms for other species.

Chapter 5 explored the use of soundscape saturation as a proxy for biodiversity and found that soundscapes varied with distance to rivers, human access points and over seasons. It is therefore important to take local landscape heterogeneity into account when comparing soundscapes across sites. We also found that higher soundscape saturation did not equate to low forest disturbance, as species that dominate the soundscape benefit more from disturbance. Wildlife captured by camera traps contributed minimally to the soundscapes, offering opportunities for combining monitoring methods to increase the overall species coverage.

Tropical forestry and wildlife conservation

In chapter 3, we showed that FSC-certified forestry is far less damaging to wildlife than non-FSC forestry as mammals were observed 43% more often in FSC-certified forest concessions than in non-FSC concessions. In particular, we observed more medium to large mammals in FSC-certified concessions: mammals in weight classes of more than 10 kg were observed 1.8 to 4 times as frequently in FSC-certified concessions as in non-FSC concessions. Furthermore, the number of Critically Endangered mammals encountered in FSC-certified concessions was four times as large as in non-FSC concessions. Lastly, we encountered fewer indications of hunting in FSC-certified concessions. The ratio of large to small mammals reveals much about the hunting pressure endured by a wildlife community, as large mammals are targeted more by hunters and recover slower from population losses (Atwood et al., 2020; Cardillo et al., 2005; Wilkie et al., 2011). Our results show that larger mammals were observed more frequently in FSC-certified concessions, providing strong evidence in support of a positive conclusion that FSC-certified forestry effectively conserves wildlife compared to non-FSC. This finding is important, as over 400 million hectares of tropical forests are designated as commercial timber concessions (Blaser et al., 2011). If all these forests were managed sustainably through FSC or similar stringent certification schemes, and hunting was controlled throughout, this would very positively affect global biodiversity conservation.

From a forest conservation perspective, the advantage of selective logging - as opposed to agro-industrial alternatives or plantation forests - is that financial value is added to standing forests, permitting economic activity while forests with a high level of structural complexity and age classes are retained. We have now shown that selectively logged natural forests with implemented FSC regulations can also retain highly vulnerable wildlife. Another advantage of FSC-certified forest forestry is that, while protected areas may struggle to find sufficient and constant funding for effective management, FSC-certified forest management guarantees some form of active ownership and management. Large mammals were present in abundance in the FSC-certified concessions, an indicator of intactness of the wildlife community, making it likely that FSC-certified forests perform conservation functions similar to well-managed protected areas (Clark et al., 2009; Edwards et al., 2014). However, this study did not compare FSC-certified concessions with protected areas, and therefore cannot draw conclusions about the degree to which wildlife communities in the sampled

FSC-certified concessions are intact compared to protected areas. Moreover, making comparisons with protected areas may not necessarily yield a representative image of ecosystem intactness in FSC-certified forest logging concessions. This is because protected areas are often also affected by human activities: examples abound of poorly managed – or even "paper" parks - where illegal logging and hunting are rife (Laurance et al., 2012; Poulsen et al., 2017). Thus, in order to make a valid comparison between logging concessions and protected areas, it should first be established what the degree of human influence and concomitant impacts are on the wildlife community in these areas. It is nonetheless important to stress that well-managed protected areas are essential for long-term conservation and that FSC-certified concessions should not be considered as a full substitute for protection of forests, yet they can be considered an addition. However, a matter of concern for FSC-certified forests is the non-permanence in ownership of concessions, as vacuums between concession holders, or subsequent concession holders who lack the ambition to achieve certification, increase the risk of degradation and forest conversion (Karsenty & Ferron, 2017).

The ability to reduce the impact of forestry on wildlife most likely lies in restricting access to infrastructure for hunters. Hunters generally do not walk further than 10 km per day in a tropical forest without roads (Froese et al., 2022), although overnight hunting camps can extend this distance (Benítez-López et al., 2017). A concessionaire may close all private roads in a concession, but it is not always realistic to assume that FSC concessionaires can effectively patrol and safeguard against hunters that enter the concession on foot or by motorized vehicles from public roads. With a well-managed private infrastructure, the periphery of the concession and the areas adjacent to public roads area are most affected by hunters entering the concession on foot. From a landscape point of view, it is important to reduce the area of this accessible 'edge' as much as possible. The shape of a concession also determines the size of the potentially affected edge area. For instance, if a concession is very narrow or small, the edge is larger relative to the entire concession area, than when a concession is round or large. FSC certification is therefore likely to have the greatest impact when forest concessions consist of large round forest blocks uninterrupted by public roads, which is something that should be considered during landscape planning. Governments in forest-rich countries can also enhance the effectiveness of protected areas by enforcing FSC certification in strategic locations like buffer zones around protected areas to reduce the edge to area ratio of the conservation landscape. Moreover, FSC-certified concessions can also be used to connect protected areas, facilitating migrations and genetic exchange (Ward et al., 2020).

In recent years, FSC was immersed in a debate about Intact Forest Landscapes (IFL), which are forests identified by satellite as relatively untouched by anthropogenic impacts and covering an area of at least 500 km^2 (Potapov et al., 2008). While some advocated that FSC-certified companies should set the IFLs in their concessions aside for conservation, others have argued that this is not feasible for companies with concessions containing large areas of IFLs. The FSC general assembly in 2022 adopted a motion which stipulates the use of landscape-wide approaches adapted to local conditions to find solutions acceptable to all relevant stakeholders. The results presented in chapter 3 may contribute to discussions to develop such landscape-wide approaches. Namely, although FSC-certified logging affects the forest, it manages to do so while preserving even the larger, more vulnerable species. However, conservation through forest certification is to some degree always compromised, as forests are intruded on by industrial activity and through the creation of a dense network of roads. Regardless of the management measures being taken to reduce anthropogenic impacts, the creation of roads is likely to always contribute to some increase in hunting pressure in comparison to intact forests. Moreover, selective logging unmistakably affects the vegetation structure and floristic species composition, as certain species are removed and other are favored by the creation of a more open forest structure (Hall et al., 2003). In summary, FSC-certified logging does not affect ecosystems as much as non-FSC logging, but it will nonetheless affect the forest. An effort should thus be made to protect IFLs, and where this is not an option, to ensure that forests are exploited by companies that are FSC-certified or have similarly stringent management schemes. If no other alternatives exist, logging companies may also seek to exploit in ways that

Box 4. Knowledge gaps in FSC-certified forest management in tropical forests

1. The impacts of FSC-certified forest management on biodiversity and ecosystem services.
2. The effectiveness of FSC-certified forest management in reducing deforestation and degradation.
3. The economic and social benefits of FSC-certified forest management.
4. The impacts of FSC-certified forest management on local communities and Indigenous Peoples.
5. The impacts of FSC-certified forest management on climate change.
6. How FSC-certified forest management should adapt to climate change.
7. The impacts of FSC-certified forest management on demand for environmentally responsibly produced products in the global timber market.
8. The effectiveness of FSC-certified forest management in promoting sustainable livelihoods.
9. The effectiveness of FSC-certified forest management in promoting sustainable forest management.
10. The effectiveness of FSC-certified forest management in promoting sustainable forest governance.

minimize impacts through ‘light-logging’ approaches, for example by avoiding the construction of logging camps with residences in IFLs, or by building primary roads around rather than through IFLs where possible.

Only 13% of the forestry concessions in Gabon and 22% in Congo are FSC-certified, totaling up to an approximate 5 million hectares, against 24 million hectares of non-FSC concessions (Eba’a Atyi et al., 2022). Our results show that FSC-certified concessions consistently harbor more large mammals than non-FSC concessions, implying that trading non-FSC timber from central Africa on international markets may result in the degradation of wildlife communities over extensive areas. However, non-FSC companies are not a uniform group, but vary along a gradient of environmental and social responsibility (Rayden & Essono, 2010). For effective management of anthropogenic pressures in logging concessions, any similarly stringent set of requirements pertaining to infrastructure management, hunting regulations, provision of alternative protein sources and other measures that resemble those of FSC, can effectuate the desired results. Effective, thorough and regular third-party auditing is likely a pivotal factor for the success of any certification scheme. For instance, national legislation related to timber harvesting and wildlife protection in our study countries does not differ much from FSC’s environmental requirements. Strong enforcement of national laws is however often lacking, as tropical forests are for the most part situated in countries with challenging environments for effective governance, ranking high on global corruption indices (Hauenstein et al., 2019; Keane et al., 2008; Smith et al., 2003). This therefore necessitates independent verification of compliance.

To date, most certification schemes remain largely unevaluated by external reviews and science. Given the plethora of certification bodies for timber and other commodities and the lack of scientific evidence, it is incredibly difficult for end-users to determine whether a certified product has a better environmental performance compared to conventional sourcing. Rigorous impact assessments through well-replicated study designs such as ours are therefore crucial to validate responsible resource production. Although chapter 3 provides an important piece of evidence on the effectiveness of FSC certification to conserve wildlife in tropical forests, there are many more knowledge gaps that merit attention from rigorous scientific studies (Box 4). Such studies will help to identify potential points of improvement and strengthen the rationale for responsible forest management.

Future perspectives for wildlife monitoring

For data-driven policy and adaptive management, it is necessary to know whether conservation-friendly interventions, whether in protected areas or in production landscapes, have the desired effect (Box 5). Unfortunately, monitoring of impacts is generally the least well implemented part of any intervention, which also accounts for forest certification schemes (Newsom et al., 2006). FSC requires that forestry concessions monitor biodiversity, but this is often not effectively executed as standard monitoring requirements are not specified and monitoring activities often lack scientific rigor (Kuijk et al., 2009), unless the monitoring is done by a third party partner NGO such as the World Wildlife Fund (WWF) or the Wildlife Conservation Society (WCS). Ambitions to overcome these challenges should come with the recognition that wildlife monitoring is expensive and that not all species, from insects to mammals, can be monitored everywhere and on a regular basis (Meijaard & Sheil, 2012). To set realistic monitoring requirements, choices need to be made regarding the target species, locations and timeframes based on local contexts. Priorities may include species that are sensitive to hunting and habitat perturbances, while generalists that adapt easily may require less attention. Streamlining monitoring requirements, but also of monitoring methods and protocols, will facilitate impact evaluations that can steer data-driven decision making.

In chapter 2, we discuss three main monitoring methods used in tropical forests, highlighting that not one method can be used to cover all species and that methods thus ideally need to be combined to monitor a broad range of species. If this is not feasible, monitoring objectives and prioritized species should be aligned with the available expertise and resources to select the most suitable monitoring method. Camera traps and acoustic methods easily gather large amounts of data, which makes automation an important priority for wildlife monitoring development. Work related to this thesis, and to which I have contributed by participating in the conceptualization and providing training data, underscores that automation of monitoring methods is a gradual process with incremental improvements in efficiency, precision and species coverage (Whytock, Świeżewski, et al., 2021). We developed a camera trap detection algorithm for species in Central Africa. The model was integrated in the user-friendly desktop application Mbaza-AI (https://appsilon.com/data-for-good/mbaza-ai/), which can now be used offline by park managers, researchers and other organizations or individuals with an interest in wildlife monitoring to automatically classify camera trap images of Central African wildlife. Currently, successful identification of camera trap images still varies considerably between species. Retraining classifiers with more data and improving the detection models with state-of the-art computer vision methods will gradually improve their capacities and thereby the applications of the software.

One such application is the development of an AI-enabled camera trap that can send real-time alerts (Whytock, Suijten, et al., 2021). This camera trap allows, for example, for the timely detection of poachers to direct eco-surveillance activities, and of detection of elephants near agricultural plots to prevent human-elephant conflict.

Box 5. The results of this study may have implications for the lives of millions of mammals

Over the whole of Central Africa, currently only 5.3 million hectares of forest concessions are FSC-certified against almost 54 million hectares of non-FSC concessions. Increased demand for FSC-certified products may raise the area of well-managed forests that provide a haven to threatened wildlife and maintain ecosystem integrity. If the data presented in chapter 3 can stimulate legislators, NGOs, businesses and end-users to increase demand for FSC-certified products just a fraction, and if this would then translate into an increase of the area of FSC-certified forests in Central Africa by just 1%, this would result in an additional half a million hectares of FSC-certified forests. Considering that we showed in chapter 3 that wildlife overall is observed 43% more often in FSC-certified concessions than in non-FSC concessions, and that animals weighing more than 100 kgs were even 4 times as abundant, this study could potentially affect the lives of millions of mammals. Quantifying impacts, and thereby validating the rationale for a certain management type, is essential and important work for effective and data driven decision making.

Using sound recorders to detect wildlife has the advantage over camera traps that detection distances are much larger, resulting in more efficient monitoring, which ultimately requires less monitoring effort, less materials and lower overall monitoring costs for vocally active species. The application of acoustic methods in wildlife monitoring is likely to transcend its current niche of highly technical and science related monitoring, becoming increasingly important as machine learning methods steadily improve. In chapter 4, we developed a classification algorithm which effectively identifies vocalizations of four primate species. Gathering and labelling acoustic training data is the most time-consuming part of developing classifiers. To gather many primate vocalizations in a short amount of time, we recorded the training data in a primate sanctuary. We then sped up the labelling process by filtering the recordings for sections with activity in the appropriate species-specific bandwidths that are likely to contain primate vocalizations. However, the recordings in the sanctuary had one drawback: they did not contain the same background noise as a tropical forest. This was remedied in a follow-up study (Zwerts et al., unpublished manuscript), where the data were pasted on background noise recorded in a nearby tropical forest. This way, we efficiently acquired large amounts of training data and enriched the dataset with a representative background. The pipeline to repeat these techniques will be published as an open-source method, allowing other researchers to efficiently gather and label training data from recordings in zoos, potentially facilitating and expediting the automation of acoustic detection of other species. We also published the training dataset in a data science challenge, allowing other teams to improve upon our classifier (Schuller et al., 2021). This yielded various new machine learning approaches and expedited the development of an effective acoustic classifier (Egas-López et al., 2021; Illium et al., 2021; Müller et al., 2021; Pellegrini, 2021). We subsequently used the challenge winning method specifically for chimpanzees and tested this on tropical forest recordings adjacent to a chimpanzee enclosure, showing its effectiveness for counting chimpanzees in the wild (Zwerts et al., unpublished manuscript). Concerted and creative approaches to developing training datasets and algorithms may enhance the detection of vocal species, and thereby improve the monitoring of species with high conservation priority.

Apart from the detection of specific species, sound recordings can also be used to analyze all the sounds in a landscape to derive proxies for biodiversity. In chapter 5, we calculated the soundscape saturation index as a proxy for biodiversity. Soundscapes varied with distance to rivers, human access points and over seasons and soundscape saturation was highly land-use type specific. Moreover, higher soundscape saturation did not equate to low forest disturbance as highly vocal species seemed to benefit from a loss of ecosystem intactness. Wildlife captured by camera traps did not correlate to soundscapes. Camera traps mostly observe mammals, while soundscapes are dominated by insects and to a lesser degree by birds. This indicates that the soundscape data and camera trap data show complementary species coverage. Although soundscape saturation showed promise in showing variation according to land-use types, it remains difficult to interpret what the changes in soundscape structure mean in terms of biodiversity. The advantage of using soundscapes is that in principle it can be used to monitor all acoustically active wildlife. However, usually a few taxonomic groups, such as insects, dominate the soundscape and thereby conceal the vocalizations of other taxa.

In this study, we only used the soundscape saturation index. Many other indices exist, each summarizing a distinct characteristic of the soundscape and thereby representing a different piece of information about the biodiversity (Buxton et al., 2018). For successful application of these indices, the challenge is to improve our understanding of how changes in biodiversity are reflected by directional changes in the various indices in varying ecological contexts, leaving a wealth of research opportunities. One potential application of soundscapes would be to quantify the rate of biodiversity recovery in reforested or restoring ecosystems, or to monitor biodiversity in forest patches and corridors in commodity monocultures or timber plantations. This may help to quantify biodiversity retention and recovery in project execution and to enforce biodiversity objectives. Soundscape research may even be extended underground to measure ground vibrations caused by large wildlife. This can be done using approaches similar to acoustic species detection and soundscape analysis. Overall, the application of sound, either for species specific monitoring or for soundscape analyses, has a multitude of possible applications that are only beginning to be explored, and can potentially be added to the toolkit of approaches for wildlife monitoring of different species in different contexts.

Not all available biodiversity monitoring methods were considered in chapter 2. One increasingly used method biomonitoring method is the use of environmental DNA (eDNA), which has so far predominantly been employed for aquatic species monitoring. However, recent developments related to airborne eDNA sampling have opened interesting possibilities for monitoring of terrestrial species in tropical forests (Clare et al., 2022; Pumkaeo et al., 2021; Roger et al., 2022). With airborne sampling, the method proved reliable for insect monitoring and even for the detection of certain vertebrate species (Lynggaard, Bertelsen, et al., 2022; Lynggaard, Froslev, et al., 2022). Moreover, eDNA was hitherto mainly used as a method to assess species presence or species richness, but recent work for aquatic environments has shown that eDNA might also provide reliable information about species abundance. These developments show that the use of eDNA can become a powerful method for biodiversity monitoring (Li et al., 2021; Spear et al., 2021; Yates et al., 2019).

Outlook on increasing the share of sustainably produced timber and the importance of wildlife monitoring

The increase of the number of FSC-certified forest concessions in the tropics has been stalling over recent years (FSC, 2022). The expected price premiums for certified wood products traded in international markets are apparently not sufficient to incentivize forestry companies to engage with FSC certification. Moreover, demand for FSC-certified products is mainly concentrated in the EU and the USA, while there is limited demand for certified timber on Asian markets. Increasing demand is important to increase the area of certified forests. Legislation in major consumer markets can have a significant impact on the demand for forest certification. For example, in the European Union, the Forest Law Enforcement, Governance and Trade (FLEGT) Action Plan requires that all timber and timber products imported into the EU must be legally harvested and verified. This is likely to positively affect the demand for forest certification, as companies must prove that their timber products are legally sourced in order to meet the requirements of the FLEGT Action Plan. More recently, the European Union set out criteria for sustainable investments in the EU Taxonomy classification system for sustainable activities. These criteria include avoiding deforestation, promoting sustainable forest management, and protecting biodiversity. The classification is designed to help investors identify investments that are environmentally sustainable. This could lead to increased scrutiny of forest certification schemes, as well as increased demand for certified products that meets the criteria set out in the law. Collaboration between major consumer markets like the USA, EU and China to strengthen legislation for the sourcing of responsibly produced timber is intensifying (Dlamini & Montouroy, 2017; Marín Durán & Scott, 2022). This is important, as China is a the world's largest importer of tropical timber (ITTO, 2020), and only coordinated sustainable sourcing between all major global markets can ensure sustainable production and biodiversity protection. Apart from the demand side, an increase of the area of certified forests can also be promoted through legislation in producer countries. Gabon, for instance, now requires that all logging companies have to become FSC-certified or else risk losing their permits.

When logging concessions are sustainably managed and timber trees are given sufficient time to recover, selective logging can - in theory - continue indefinitely. To ensure future harvests, logging companies must respect minimum harvest diameters and maintain seed trees for sufficient regeneration (de Freitas & Pinard, 2008; Schulze et al., 2008). However, an important issue for the sustainability of tropical logging is whether harvest cycles and intensities are adequate to safeguard future timber stocks. Research indicates that this currently not the case (Piponiot et al., 2019; Putz et al., 2012; Roopsind et al., 2017; Shearman et al., 2012; Sist et al., 2021; Zimmerman & Kormos, 2012). Logging companies can boost regeneration and growth rates through enrichment planting and pre- and postharvest management measures, although such measures are expensive when discounted over the duration of harvest cycles (Cropper Jr & Putz, 2017; Peña-Claros et al., 2008; Schwartz et al., 2013). Sustainability may be improved by exploiting more timber species, extending harvest cycles or by reducing maximum harvest volumes. In the latter two cases, finding other sources of revenue for forestry concessions may help in maintaining profitability. This could be realized by new and more diverse forest management approaches, which may include enhanced labor opportunities for local communities and seeking other sources of revenue such as non-timber forest product collection (Karsenty & Vermeulen, 2018).

In chapter 3 we showed that in FSC-certified forestry concessions, effectively more elephants were encountered in comparison to non-FSC, which might be translated into an additional revenue stream for concessionaires because of the demonstrated linkages between elephants and carbon storage in tropical forests (Berzaghi et al., 2022). Standing forests provide a range of ecosystem services, such as regulating water cycles, carbon storage and harboring biodiversity (Bonan, 2008; Brandon, 2014; Ellison et al., 2012). Adequately valuing and monetizing these ecosystem services, and developing systems in which the beneficiaries pay for them in Payments for Ecosystem Services (PES) schemes can help raise funding for conservation of forests. By providing additional sources of revenue for standing forests, PES schemes can strengthen the incentive to avoid deforestation and degradation and numerous funding mechanisms for PES schemes already exist (Farley & Costanza, 2010; Ingram et al., 2014; Jayachandran et al., 2017; Salzman et al., 2018; Wunder et al., 2008).

As international cooperation on biodiversity conservation strengthens and associated policies mature, corporate involvement in such schemes is likely to increase (Krause & Matzdorf, 2019). For instance, the EU Corporate Sustainability Reporting Directive (CSRD) requires increasingly more companies to report on their environmental business impacts (Lucarelli et al., 2020; Schütze et al., 2020). Moreover, the EU Directive on Corporate Sustainability Due Diligence (CSDD) requires companies to identify and prevent potential adverse impact of their activities on human rights and the environment by integrating due diligence in their policies (Mak, 2022). Such regulations are assumed to progressively stimulate companies to either avoid, reduce or offset the impact of their business operations. Compensation of negative impacts will for instance raise the demand for carbon credits, which tropical forest rich countries can generate by preventing deforestation, providing a cost-effective way to fight climate change (Strassburg et al., 2012). Through similar mechanisms, companies could improve their environmental impact by buying biodiversity credits that can be sold by entities that effectively conserve biodiversity (Alvarado-Quesada et al., 2014; Koh et al., 2019). Biodiversity or other ecosystem-related credits may not only satisfy regulatory requirements related to environmental impacts or offsets by companies, but may also have value for public relations and marketing. However, biodiversity conservation through anything resembling a biodiversity credit system will only work if animal populations can be monitored in a standardized way and with sufficient precision to allow for the detection of changing population trends. Quantifying impacts on wildlife species abundance and other changes in biodiversity makes payments for the protection of biodiversity more transparent, verifiable, concrete and better understandable (Krause & Matzdorf, 2019). To do this cost-effectively, automation of wildlife monitoring methods is a prerequisite, representing a highly pressing knowledge gap to be addressed (Chapter 2).

In Central Africa, large swaths of tropical forests are designated for timber extraction, and our results have shown that there is much to be gained with effective management that prevents the degradation of these forests. Our results can however not simply be extrapolated to forest certification in other regions around the world. Effectiveness of any set of requirements depends on socio-economic context, logging intensity, forest size, and drivers of deforestation and degradation, which all vary widely across continents. For all other production landscapes, ecosystems, commodities and conservation projects, it is important to acquire data on the effectiveness of interventions, to enable data driven decision making and evidence-based policies. To evaluate impacts and quantify biodiversity effectively, innovative and multimethod monitoring approaches are required. The continued development of standardized and automated methods that can capture changes in biodiversity with increasing precision is important to support the conservation of biodiversity in natural and production landscapes.

The frequent call for the conservation of tropical forests should be met with the realism that economic benefits have historically typically been prioritized over nature conservation. Providing economic incentives for sustainable management of tropical forests is therefore pivotal for their conservation. Certified forest management allows for economic activity, while preserving standing forests and addressing and mitigating negative environmental and social impacts of the forestry operations. FSC certification, or similar stringent schemes, should therefore become the norm in the forestry industry. It should furthermore not only depend on consumers' choices, but also become a governments' responsibility to ensure sustainable timber production and conservation of biodiversity.

The bottom line is that if we want to retain the natural world while securing the provisioning of commodities, these resources *must* be produced sustainably. Sourcing tropical timber can be done sustainably through strict certification schemes, and it is imperative that governments implement sustainable-only policies, that these policies are rigorous, and that their expected impacts are quantified and validated.

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Dutch summary - Samenvatting

Tropische bossen herbergen het grootste deel van alle terrestrische biodiversiteit, waaronder 62% van alle terrestrische gewervelde soorten. Van de resterende tropische bossen is meer dan een kwart aangewezen als houtkapconcessies, wat mogelijk negatieve gevolgen heeft voor de biodiversiteit in deze bossen. Boscertificeringsorganisaties zoals de Forest Stewardship Council (FSC) beweren dat ze bedreigingen voor de biodiversiteit aanpakken, maar studies hebben tot op heden niet geleid tot een robuuste verificatie van de effecten van gecertificeerde houtkap op de biodiversiteit vanwege beperkingen in onderzoeksopzet en schaal. Het meten van impact is belangrijk voor geïnformeerde besluitvorming en data-gedreven beleid. Hiervoor is betrouwbare populatiemonitoring essentieel. Het doel van dit proefschrift is om te beoordelen of dieren effectiever worden behouden in FSC-gecertificeerde houtkapconcessies dan in niet-FSC-concessies, en om te onderzoeken hoe populaties van wilde dieren in tropische bossen het best kunnen worden gemonitord. Ik begin dit proefschrift door de drie belangrijkste monitoringmethoden te vergelijken om richtlijnen op te stellen voor het monitoren van wilde dieren in tropische bossen. Vervolgens onderzoek ik de kennislacune met betrekking tot de effecten van FSC-gecertificeerde bosbouw, door te beoordelen of dieren in het wild effectiever worden beschermd in FSC-gecertificeerde houtkapconcessies dan in niet-FSC-concessies.

De data voor dit onderzoek zijn verzameld met behulp van cameravallen in veertien bosbouwconcessies in West-Equatoriaal Afrika. Ik ontdekte dat FSC-gecertificeerde bosbouw gunstig is voor zoogdieren in vergelijking met niet-FSC-bosbouw, met de meest uitgesproken positieve gevolgen voor zoogdieren die 10 kg of meer wegen. Vervolgens ontwikkel en test ik twee methoden voor het monitoren van dieren in het wild: het gebruik van geluid voor het monitoren van primaten en het gebruik van soundscapes als proxy voor de algehele biodiversiteit in een bos. Soort-specifieke monitoring met geluid heeft als voordeel dat andere soorten gemonitord kunnen worden dan met cameravallen. Geluidsmonitoring vereist echter geautomatiseerde classificatie om bruikbaar te zijn. Voor soundscapes is de interpretatie van veranderingen in de soundscape en de kwantificering van de bijdragen van individuele soorten de grootste uitdaging, evenals de relatie tussen de structuur van de soundscape en de heterogeniteit van het lokale landschap. Verdere ontwikkeling en verbetering van methoden voor het monitoren van wilde dieren is essentieel voor impact verificatie en verbetering van boscertificering. Verbeterde monitoringstechnieken kunnen ook helpen bij de ontwikkeling van betalingen voor het behoud van biodiversiteit, wat mogelijk nieuwe inkomstenstromen voor natuurbehoud oplevert.

French summary - Résumé

Les forêts tropicales abritent la plus grande part de toute la biodiversité terrestre, dont 62 % de toutes les espèces de vertébrés terrestres. Parmi les forêts tropicales restantes, plus d'un quart sont désignées comme concessions forestières, mettant potentiellement la faune en danger. Les systèmes de certification forestière comme le Forest Stewardship Council (FSC) affirment qu'ils traitent des menaces à la biodiversité, mais les études n'ont pas abouti à ce jour à une vérification solide des impacts de l'exploitation forestière certifiée sur les communautés fauniques en raison des limites de la conception et de l'échelle de la recherche. La mesure de l'impact est importante pour une prise de décision éclairée et des politiques fondées sur des données. Pour cela, un suivi fiable de la population est un préalable. Dans cette thèse, les objectifs généraux sont d'évaluer si la faune est plus efficacement conservée dans les concessions forestières certifiées FSC que dans les concessions non FSC, et d'explorer comment les populations d'animaux sauvages peuvent être mieux surveillées dans les forêts tropicales. Je commence cette thèse en examinant les applications des trois principales méthodes de surveillance pour fournir des orientations sur la surveillance de la faune dans les forêts tropicales. Ensuite, j'examine le manque de connaissances concernant les impacts de la foresterie certifiée FSC, en évaluant si la faune est plus efficacement conservée dans les concessions forestières certifiées FSC que dans les concessions non FSC.

Les données ont été recueillies à l'aide de pièges photographiques dans quatorze concessions forestières d'Afrique équatoriale occidentale. J'ai découvert que la foresterie certifiée FSC profite aux mammifères par rapport à la foresterie non FSC, avec les impacts positifs les plus prononcés pour les mammifères pesant 10 kg et plus. Ensuite, je développe et teste deux méthodes de surveillance de la faune : l'utilisation du son pour la surveillance des primates et l'utilisation de paysages sonores comme indicateur de la biodiversité globale dans une forêt. La surveillance spécifique à l'espèce à l'aide du son couvre une gamme d'espèces différente de celle des pièges photographiques. Cependant, la surveillance sonore nécessite une classification automatisée pour être utile. Pour les paysages sonores, l'interprétation des changements dans le paysage sonore et la quantification des contributions de chaque espèce sont les principaux défis, ainsi que l'interprétation de la relation entre la structure du paysage sonore et l'hétérogénéité du paysage local. Le développement et l'amélioration des méthodes de surveillance de la faune sont essentiels pour la vérification de l'impact et l'amélioration de la certification forestière. Des méthodes améliorées de surveillance de la faune peuvent également contribuer au développement de systèmes de crédit pour la biodiversité, générant potentiellement de nouvelles sources de revenus pour la conservation.

Acknowledgements

Academic life embodies the freedom to work on one's own ideas and to contribute to something valuable, which I consider a great luxury. It requires creativity to find solutions and skills as diverse as the species that I observed on my camera traps. For this PhD I had to learn a new language, I worked with people from vastly different backgrounds and cultures, I learned to navigate collaborations with international organizations and I had to secure the funds to make it all possible. I became an expert in the literature of my field, did complex data analyses, but also did physically and mentally challenging fieldwork. It is evident that I could have never done all of this alone. Hundreds of people, from dozens of nationalities and organizations, have contributed to this research. Although I am thankful to all of them, I wish to highlight several important people in particular.

First and foremost I would like to express my deepest gratitude to Marijke van Kuijk. You have been the cornerstone of this research ever since we first met in Suriname to discuss the initial research proposal. You were always available to discuss ideas and concerns and was always swift to reply with spot-on feedback. You really taught me the fine skills of being an academic and we had a lot of good laughs while doing so. I greatly appreciate your insights and experience and I think we really make a great team by complementing each other's strengths. It has been enormously pleasant to work with you and it will be a great privilege to continue to find new and exciting research opportunities together.

Liesbeth Sterck, many PhD students struggle with inaccessible promotors, but I am not one of them. I would like to sincerely thank you for always being available for a talk, a short meeting or a phone call to give advice. But most of all, I would like to thank you for being the cheerful and enthusiastic person that you are. You always kept oversight of my supervision and a keen interest into my research topics, even though they were at times quite different from your normal line of research.

Pita Verweij, thank you for your wise and thoughtful words with which you always hit the right chord. What I particularly appreciate about you is that whenever I ask you for help, you really take a deep dive into the question and carefully formulate your answers, which was of great help to me. You also motivated and inspired me to seek media attention for the successes in my project, which showed me that outreach is an invaluable part of being a scientist and which I will continue to pursue.

Fiona Maisels, I think your spontaneous decision to join us to a Roger Waters concert after I invited you to come to Utrecht as a speaker on the wildlife monitoring symposium says it all. After the symposium, you also proposed to become a co-promotor of my PhD. I really appreciated this, as your endless knowledge about wildlife and African tropical forests provided a wealth of important information. Thank you for your eye for detail, for being such a warm-hearted person, and for being able to cope with an all Dutch team.

Jaap van der Waarde, you are the most experienced and driven conservation biologist that I know and you have been a great inspiration to me. Without your initiative, ideas and support, this thesis would have never existed. It has always been a great pleasure to work with you, travel with you to remote places in the tropical forests of Cameroon, and to hear your thoughts and ideas about the future of conservation and related research opportunities. You taught me to think big and always managed to surprise me with your bird's-eye view of anything related to wildlife and tropical forests. You showed me, through your inexhaustible resilience, how to deal and overcome the day to day hurdles of working in the Congo Basin with a smile and to use frustrations as a starting point for new ideas. I want to sincerely thank you for your belief in me and for supporting my research.

George Belmond Tchoumba, un grand merci pour la très agréable collaboration. At the start of my project, I had little to no experience with working in Africa and still had to learn much about our cultural differences. You helped me in this process by always being understanding and patient, by maintaining a positive mindset and by continuing to look ahead. I always deeply admired your eloquence and capacity to summarize complex issues in concise and clear language. It was always a great pleasure to see you in the WWF office whenever I was in Yaoundé, and it was an even greater pleasure to see you at the FSC general assembly in Bali, where seeing you work served as a crash course in diplomacy and politics to me.

Hermann Donfouet Zebaze, my unshakeable partner in the field. We travelled thousands of kilometers to visit logging companies across Western Equatorial Africa. You were invaluable in helping me to manage the logistics, materials and the hundreds of locally recruited employees. I would have never managed to complete all the fieldwork without you. Managing this extensive project in some of the most remote corners of Africa was, at times, very difficult. We have gone through some tough situations in the field and on the road but you were never much perturbed by any of it. For instance, there were times without water for cooking, drinking or bathing while camping in the forest at night, and other times with too much water, which forced us to wade through chest deep swamps in the pouring rain. But whatever the challenge, you always maintained a big, heartfelt smile on your face. Apart from all the practical work that you did with great precision and calm, I learned a lot about life from you, about

African culture, about resilience and acceptance in the face of setbacks and struggles, about confidence and trust in each other and about life in general, and I would like to thank you for that.

I want to acknowledge the 263 locally recruited employees for their hard work as porters, trackers, cooks and drivers during the field missions. The conversations we had during long hikes in the jungle, or when sitting next to the campfire at night while being immersed by the sounds of numerous creatures, taught me so much about the forest, about edible plants and mushrooms and about our different cultures. Many of you I will never forget, and I would like to express my most sincere gratitude for the received friendliness and openness, and the connection we made.

I also want to thank the collaborating logging companies who provided access to their concessions, which enabled me to do this research. It was not always easy to connect to yet another company to pursue my research objectives, but I was often warmly welcomed by the people I encountered. Meeting these often highly passionate people provided me with a unique insight into the day to day life and work of running a business in the distant forests of Western Equatorial Africa.

I am also grateful to all my colleagues from the Ecology and Biodiversity group, and especially my roommates Rens Vaessen and Martin Droog for the good time we had at the office. I also want to thank George Kowalchuk for making me feel welcome in the group and being a fun and accessible professor.

I then wish to show gratitude to the people from the all the WWF offices that I visited and worked with and who helped me to with the necessary paperwork, finances and logistics. I also wish to thank ZSL Cameroon, where the people always welcomed me and helped me with much practical knowledge about camera trapping. And especially Tom Bruce, thanks for the great fun we had when we were sharing an apartment in Yaoundé. I furthermore thank the bio-acoustics team for the fantastic work we did together that taught me so much about machine learning and computer vision. Unmistakably, I wish to thank the forty students that have contributed to the research in this thesis.

I particularly wish to thank Jelle Backx, for your friendship, your enthusiasm about my work, and the in-depth conversations about research during our lunch walks. I am also grateful to Rens de Weert, Bas van der Hoek, Maarten Jalink and Lidwien Swenker for taking the initiative to come Gabon to see what my work in the jungle was really like.

Then finally, I wish to express my deepest gratitude to my family, who gave me the wisdom and dedication to do this work and who were always there for me with their unwavering love and support. You bravely travelled after me, first to Suriname, and then to Gabon, to pick up a machete and join me deep into the forest.

Dad, you instilled my attraction to nature by sharing your own deep-rooted fascination for the natural world while hiking with me through the Ardennes, canoeing in Norway and on countless other wonderful holidays. I once asked you what you would have wanted to do if you could do anything you want. You said that, if you would have gotten the chance, you would have loved to have done research in tropical forests. This remark always stayed in the back of my mind and formed part of the inspiration to pursue this dream career. Thank you for that.

Mam, thanks for being the most caring and supportive mother in the world. You would do anything to help me succeed and be happy. You always motivated me to work hard and I knew that it would make you proud. But there was never any pressure, as long as I promised to stay safe.

The last words are for my beloved Joukje. Thank you for your patience while I was far away in the forest, your encouragement and thoughtful advice when I needed it, and your radiating optimism, enthusiasm and love, which always gave me a reason to go back home with a smile.

Publications, outreach and funding

Journal articles

1. Zwerts et al., FSC-certified forestry benefits large mammals compared to non-FSC, *Nature, in revision.*
2. Whytock, R. C., Suijten, T., van Deursen, T., Świeżewski, J., Mermiaghe, H., Madamba, N., Mouckoumou, N., Zwerts, J. A., Pambo, A. F. K., Bahaa-el-din, L., Brittain, S., Cardoso, A. W., Henschel, P., Lehmann, D., Momboua, B. R., Makaga, L., Orbell, C., White, L. J. T., Iponga, D. M., & Abernethy, K. A. (2023). Real-time alerts from AI-enabled camera traps using the Iridium satellite network: A case-study in Gabon, Central Africa. *Methods in Ecology and Evolution*, *n/a*(n/a). https://doi.org/https://doi.org/10.1111/2041-210X.14036
3. Zuidema, P. A., & Zwerts, J. A. (2022). An energetic look at the life in logged forests. *Nature Publishing Group.*
4. Zwerts, J. A., Wiegers, J. N., Sterck, E. H. M., & van Kuijk, M. (2022). Exploring spatio-temporal variation in soundscape saturation of an African tropical forest landscape. *Ecological Indicators*, 137, 108712. https://doi.org/10.1016/J.ECOLIND.2022.108712
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9. Whytock, R. C., Świeżewski, J., Zwerts, J. A., Bara-Słupski, T., Koumba Pambo, A. F., Rogala, M., Bahaa-el-din, L., Boekee, K., Brittain, S., Cardoso, A. W., Henschel, P., Lehmann, D., Momboua, B., Kiebou Opepa, C., Orbell, C., Pitman, R. T., Robinson, H. S., & Abernethy, K. A. (2021). Robust ecological analysis of camera trap data labelled by a machine learning model. *Methods in Ecology and Evolution*, 00, 2041-210X.13576. https://doi.org/10.1111/2041-210X.13576
10. Zwerts, J. A., Stephenson, P. J., Maisels, F., Rowcliffe, M., Astaras, C., Jansen, P. A., van Der Waarde, J., Sterck, L. E. H. M., Verweij, P. A., Bruce, T., & van Kuijk, M. (2021). Methods for wildlife monitoring in tropical forests: Comparing human observations, camera traps, and passive acoustic sensors. *Conservation Science and Practice*, 3(12), e568.
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14. Zwerts, J.A., Introduction chapter. Lianas of the Guianas by Hoffman and Ruysschaert, 2017.
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Conference proceedings

1. Zwerts, J.A. 2022. FSC General Assembly. Does FSC certified forestry help to conserve wildlife in tropical forests? Bali, Indonesia.
2. Zwerts, J.A. 2022 September. Presentation and poster. Netherlands Annual Ecology Meeting, FSC-certified forestry benefits large and critically endangered wildlife compared to non-FSC. Lunteren, The Netherlands.
3. Zwerts, J.A. 2022. Plenary address UU Conference Data Science & AI for Society. Just listen: automated acoustic monitoring of chimpanzees. Utrecht University.

Outreach and valorization

1. Interview & WWF magazine article - Zwerts, J.A. 2023, Maart. 'Tuinman in de Jungle'. WWF Magazine article about the role of Forest Elephants in forest ecology and carbon sequestration. https://magazine.wwf.nl/magazine-februari-2023/tuinman-van-de-jungle
2. Presentation - Zwerts, J.A. 2023 March. VolkerWessels (2nd largest construction company of the Netherlands), Olifanten beschermen in de bouwmarkt. Vianen, The Netherlands.
3. Presentation - Zwerts, J.A. 2023 January. Ministerie van Landbouw, Natuur en Voedselkwaliteit (LNV), Protecting Elephants in the Hardware Store. The Hague, The Netherlands.
4. Presentation - Zwerts, J.A. 2022 December. Knowledge session about the wildlife conservation value of FSC-certified forests. WWF, Zeist, The Netherlands.
5. Presentation - Zwerts, J.A. 2022 December. Tetrapak International sustainability strategy. How to evaluate impacts? Online.
6. Presentation - Zwerts, J.A. 2022 November. Partnership for Biodiversity Accounting Financials (PBAF). Does FSC certified forestry help to conserve wildlife in tropical forests? Online.
7. Interview & news article - Zwerts, J.A. 2022 November. News article about my experience and contribution to the FSC General Assembly 2022 in Bali, Indonesia.
8. Dutch: https://www.uu.nl/nieuws/bioloog-joeri-zwerts-ervaart-impact-van-zijn-biodiversiteitsonderzoek-tijdens-internationale-fsc
9. English: https://www.uu.nl/en/news/biologist-joeri-zwerts-experiences-the-impact-of-his-biodiversity-research-at-global-fsc-meeting
10. Presentation - Zwerts, J.A. 2022 October. Wildlife film festival, Does FSC certified forestry help to conserve wildlife in tropical forests? Rotterdam, The Netherlands.
11. Expert Panel - Zwerts, J.A. September 2022. Biodiversity Expert Roundtable. Precious Forests Foundation. Switzerland, Online.
12. Presentation - Zwerts, J.A. September 2022. Knowledge session at Wageningen University about the proceedings of my PhD. Wageningen University, The Netherlands.
13. Guest lecture - Zwerts, J.A. September 2022. Dutch tropical forest association. Does FSC certified forestry help to conserve wildlife in tropical forests? Utrecht, The Netherlands.

14. Keynote address - Zwerts, J.A. 9 June 2022. FSC event. Does FSC certified forestry help to conserve wildlife in tropical forests? Putten, The Netherlands.
15. Interview & news article - Zwerts, J.A. 11 April 2022. How data science can help wildlife. Utrecht University. https://www.uu.nl/en/news/how-datascience-can-help-wildlife
16. Presentation - Zwerts, J.A. 2021. Preliminary results of the FSC impact study and side projects. WWF Cameroon, Yaoundé, Cameroon.
17. Presentation - Zwerts, J.A. 2021. Wildlife monitoring in the Congo Basin. WWF, Zeist, The Netherlands.
18. Interview Zwerts, J.A. , 6 October 2020. Verantwoord bouwen met hout. Hoe dan? Muntgebouw, Utrecht, The Netherlands. https://www.cirkelstad.nl/verantwoord-bouwen-met-hout-hoe-dan/
19. Interview & news article - Zwerts, J.A. 20 July 2020. "The collaboration with research engineers and data experts has made this a much more interesting research project". Utrecht University. https://www.uu.nl/en/news/the-collaboration-with-research-engineers-and-data-experts-has-made-this-a-much-more-interesting
20. Interview & news article - Zwerts, J.A. 1 July 2020. Tropical forests can handle the heat up to a point. Utrecht University. https://www.uu.nl/en/news/tropical-forests-can-handle-the-heat-up-to-a-point
21. Interview & news article - Zwerts, J.A. May 2020. Een kijkje bij het onderzoek van Joeri Zwerts. Nieuwsblad Vereniging Tropische Bossen.
22. Interview & news article - Zwerts, J.A. June 2019. Groen Afrika. WWF Magazine. https://magazine.wwf.nl/magazine/groen-afrika
23. Interview & news article - Zwerts, J.A. 2 februari 2019. Zoogdieren lopen massaal in de cameraval. Bionieuws.
24. Guest lecture - Zwerts, J.A. 2019. Utrecht U-Talent program. Natuurbescherming in de tropen. Utrecht, The Netherlands.
25. Guest lecture - Zwerts, J.A. 2019. Wageningen University. Wildlife conservation in intact versus managed tropical forests. Wageningen, The Netherlands.
26. Guest lecture - Zwerts, J.A. 2019. University of Amsterdam. Wildlife conservation and resource production; are they reconcilable? Amsterdam, The Netherlands.
27. TV documentary - NPO1, 4 October 2018.Television documentary on the research of Joeri Zwerts with Art Rooijakkers. Helden van de Wildernis - Congo. NPO1. https://www.npostart.nl/helden-van-de-wildernis/04-10-2018/AT_2103690 https://www.avrotros.nl/helden-van-de-wildernis/gemist/detail/helden-van-de-wildernis-congo-04-10-2018/
28. Guest lecture - Zwerts, J.A. 2019. Honours Program at Varendonck College. Een kijkje in de keuken van de natuurbescherming. Asten, The Netherlands.
29. Guest lecture - Zwerts, J.A. 2018. Wageningen University. Wildlife conservation in intact versus managed tropical forests. Wageningen, The Netherlands.
30. Symposium - Joeri Zwerts & Marijke van Kuijk, 18 June 2018. Organizers of the symposium 'Animal Monitoring in Tropical Forests' in collaboration with WWF NL and 'The Prince Bernhard Chair for International Nature Conservation'. Utrecht University.
31. Interview & news article - John O'Connor and Joeri Zwerts, 14 February 2017. Two more positions in the NWO graduate program on 'Nature Conservation, Management and Restoration' filled. Utrecht University. https://www.uu.nl/en/news/two-more-positions-in-the-nwo-graduate-program-on-nature-conservation-management-and-restoration

MSc projects supervised

1. Westland, D. 2022. Density depending effects on mammalian activity patterns in the Congo Basin. Master's thesis. Utrecht University.
2. Geelen, E. 2021. The impact of FSC certification on wildlife conservation in tropical forests. Master's thesis. Utrecht University.
3. Nair, P. 2021. The effect of FSC certification on wildlife conservation. Master's thesis, Utrecht University.
4. Rothengatter, A.M.J. 2021. Comparison of Camera Trap Distance Sampling (CTDS) and the Space to Event model (STE) for estimating population densities of medium to large animals in a Tropical Forest. Master's thesis, Utrecht University.
5. Alves, J.C.T. 2020. A non-metric multidimensional scaling analysis of species abundance in the Congo basin. Mini-project Master, Utrecht University.
6. Brouwer, E. 2020. The Influence of Leopards on the Activity Patterns of African Forest Antelopes: Perceptible by Camera Traps? Mini-project Master, Utrecht University.
7. Ploem, J. 2020. Evaluation of the space to event model for five Central African duiker species in Gabon. Master's thesis, Utrecht University.
8. Van Herwijnen, A. 2020. Implications of FSC-certified forestry for relative abundance and temporal behaviour of mammals in Central African tropical rainforests. Master's thesis, Utrecht University.
9. Wiegers, J.N. 2020. Assessing acoustic diversity in a logged Afrotropical rainforest using soundscape analysis. Master's thesis, Utrecht University.
10. Van den Berg, J. K. 2019. Evaluation of distance sampling with camera traps for three Central African mammalian species. Master's thesis, Utrecht University.
11. Zlatev, D. 2018. Case study on the use of the defaunation index to analyze camera trap data from a Central African rainforest. Master's thesis, Utrecht University.

Other impacts

1. 2022. IUCN forest elephant range has been expanded based on the data gathered for this thesis.
2. 2022. IUCN giant forest hog range has been confirmed with the data gathered for this thesis.
3. 2022. The results of my PhD thesis influenced top priority policy discussions concerning intact forest landscapes and related policy decisions during the FSC General Assembly in Bali, Indonesia.

Grants and prices

1. Joeri Zwerts, €29.000, Word Wildlife Fund (WWF) The Netherlands, for post-doc research (2022).
2. Joeri Zwerts, €5000, Applied Data Science Grant, to initiate a multidisciplinary project between ecology and computer sciences at Utrecht University (2020).
3. Joeri Zwerts, €90.000, Programme de Promotion de l'Exploitation Certifiée des Forêts (PPECF) of the Commission des Forêts d'Afrique Centrale (COMIFAC), de la COMIFAC (through KfW), for the implementation of my PhD project (2019).
4. Joeri Zwerts, €10.000, The PE&RC Interinstitutional Collaborative Grant, for collaboration between Utrecht and Wageningen University (2018).
5. Joeri Zwerts, €7.500, Word Wildlife Fund (WWF) Germany, for the implementation of my PhD project (2018).
6. Joeri Zwerts, €100.000, Word Wildlife Fund (WWF) The Netherlands, for the implementation of my PhD project (2017).
7. Joeri Zwerts, 4-year PhD position, Graduate programme "Nature Conservation, Management and Restoration", Dutch Research Council (NWO) (2017).

8. Joeri Zwerts, €5.000 for resampling of permanent forest plots through a new collaboration between Leeds University and CELOS (2015)
9. Joeri Zwerts, Willem Barentsz Award €150, for best fieldwork leading to a Master's thesis. Resource Ecology Group of Wageningen University (2013).

About the author

Joeri Zwerts was born in Eindhoven, the Netherlands. He obtained a BSc degree in Biology at Utrecht University and a MSc degree, passed with distinction (*cum laude*), in Forest and Nature Conservation at Wageningen University. His MSc thesis research was published in a peer-reviewed journal. Subsequently, he worked for two years as a forestry researcher in Suriname at the CELOS research institute. After returning to the Netherlands he wrote a research proposal to investigate the impact of FSC-certified forestry on wildlife conservation in the Congo Basin and was awarded a PhD position at Utrecht University in close collaboration with the World Wildlife Fund (WWF).

As a researcher, Joeri is particularly interested in wildlife conservation in tropical forests. He is an expert in wildlife monitoring and his research aims to develop an understanding of the linkages between land use change, management and biodiversity conservation in multifunctional agro-commodity landscapes. While working on three continents, Joeri has gained extensive experience in managing international research projects. He is convinced that science should be well-grounded in society and valorization of research outcomes is a key priority for him. He has, to this end, presented his research at events with wide ranging audiences, such as at the wildlife film festival, for multinationals, impact investors, high schools and non-governmental organizations. Additionally, a television documentary has been made about his work in the Congo basin. For Joeri, good relationships between colleagues are the cornerstone for high quality, enjoyable and productive science. Joeri is passionate about teaching and has a Basic Teaching Qualification (BKO). He developed and coordinated multiple BSc courses, and supervised over forty students.

In his free time, Joeri enjoys endurance sports and exploring the outdoors and travel. He is an avid reader and loves to spend time playing board games with friends. Joeri is currently employed as a researcher and lecturer at Utrecht University, is married and lives in Utrecht with his wife.