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Climate change direct and indirect impacts on biodiversity in the Congo Basin: a multi-dimensional approach

PhD dissertation

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Acknowledgments

« *La pirogue n'avance pas sans pagaie* ».
Bantu proverb

About four years ago, I learned about the riches of the Congo Basin through the words of Kenyan biologist, environmentalist, writer and Nobel Peace Prize laureate Wangari Maathai, in her book "*The challenges for Africa*". Then Goodwill Ambassador for the Congo Basin Forest Ecosystems, she traveled the world advocating for the protection of its vast systems of forests, rivers and swamps, and deep cultural heritage - not only for the people that call it home but also the whole planet. A seed was sown, and I had set a foot onto the pirogue. At the time, I was unaware of the depth of the scientific journey that I was embarking on, nor everything that I would need to learn in order to, both figuratively and literally, navigate it.

A special thanks goes to my two supervisors, Carlo and Sandrine, who joined me on this journey. Sandrine, I am grateful for your unabated generosity, passion for biocultural conservation and availability, even from distance. Carlo, I learned a lot from your clear vision and ability to craft compelling scientific stories. You both created a space for exploration, taught me how to weave ideas together and provided me with the proper tools to keep the boat moving.

When multiple people paddle together, the pirogue moves faster and reaches farther. I am grateful for the many, sometimes unexpected, collaborations that arose in the last years: colleagues from the GMA lab at Sapienza University, the LICCI group in Barcelona, the WCS Lac Télé team, the INRET in Gabon, the Marien Ngouabi University in Brazzaville, and the NMBU in Norway. To the friends I made along the way in Italy, Spain, Gabon, and Congo: merci, grazie, gracias, *na tondi yo*!

To friends from Lac Télé: your resourcefulness will be a source of inspiration for life. As I practiced keeping my equilibrium on tiny pirogues with you (not the easiest thing with a recovering knee!), I also learned about adaptability, attuning my ears to environmental cues and natural rythms, and realizing that, in the end, things do fall into place. Thank you for allowing me as your "student", for welcoming me in your homes, trusting me with your stories, and for the tons of makemba and ngolo fish. Célie, from flooded forests and houses, village dances, fire stories, through grief and joy, we survived a particularly intense time together. This work is also yours.

A pirogue cannot move without support. Thank you to my family, which taught me first about curiosity for the world, dedication and perseverance, and which helped me keep course when I thought that the boat was sinking. It looks like I joined you as an academic after all. Thank you to my dear friends, who inspire me and listened to all my stories from far away without fail. For all of you, here mentioned by named or not, I am grateful.

Pirogue approaching a Uapaca tree (*Uapaca* spp.). Photo by M.B.

Executive summary

Spanning 2.87 million km^2 across six Central African countries (Cameroon, the Central African Republic, the Democratic Republic of the Congo, Equatorial Guinea, Gabon and the Republic of Congo), the Congo Basin is the world's second-largest continuous tropical rainforest after the Amazon. Hosting diverse habitat types (e.g. savannas, *terra firma*, swamps or seasonally flooded forests), the Congo Basin is ranked third in terms of global species richness and support exceptional levels of biodiversity, including charismatic, endangered megafauna such as the African forest elephant (*Loxodonta cyclotis*), western lowland gorilla (*Gorilla gorilla gorilla*), central chimpanzee (*Pan troglodytes troglodytes*) or bonobo (*Pan paniscus)*. Due to its vast carbon stocks, the region has global significance in terms climate regulation, storing approximately 29 petagrams of carbon in its peatlands alone, alongside substantial above-ground biomass in its forests.

However, Congo Basin rainforests also face multiple threats, including deforestation and forest degradation driven by small and large-scale agriculture, and extractive industries such as logging, mining or oil production, alongside illegal wildlife trade. Climate change is expected to further exacerbate these pressures, with profound consequences for both biodiversity and Congo Basin human populations, many of whom depend on forest resources for subsistence. Despite its ecological and climatic importance, the region remains critically under-researched: a lack of long-term monitoring, extensive temporal and spatial gaps in instrumental data and the scarcity of field studies result in the frequent exclusion of the Congo Basin from regional and global climate and biodiversity assessments. Given the trajectory of other globally significant rainforests under climate change, it is imperative to investigate how climate change is impacting the Congo Basin and will continue to do so in the future.

Addressing this critical knowledge gap, this PhD research aims to enhance the understanding of climate change's direct and indirect impacts on biodiversity in the Congo Basin, using a multi-scalar and interdisciplinary approach. Direct impacts refer to, for example, shifts in species distributions, altered phenological patterns or disrupted trophic networks, while indirect impacts encompass human adaptation responses that may compound existing threats to biodiversity. This study is guided by three primary objectives: 1) to assess climate change impacts on biophysical systems across multiple spatial scales, 2) to identify local adaptation responses in response to climate change and their associated indirect effects on biodiversity, and 3) to evaluate climate change impacts on a keystone species, the African forest elephant.

My first analytical chapter, entitled "*Uncertain future for Congo Basin biodiversity: A systematic review of climate change impacts*", systematically reviewed current and projected climate change impacts on biodiversity at all organizational levels, from genes to ecosystems. The findings reveal widespread effects, including increased species vulnerability to extinction, shifts in species distributions and reductions in organism body size, while studies on species genetics, physiology and phenology remain scarce. Research combining climate change with other drivers of change, such as land-use change or human adaption responses, projects a bleak outlook in terms of Congo Basin biodiversity persistence. However, substantial knowledge gaps remain, particularly concerning population dynamics, shifts in plant resource availability and large-scale compositional changes. This review underscores the urgent need for further research to address these deficiencies.

In my second analytical chapter, "*"We saw fish in the cocoa farm": Local observations of the impacts of climate change on biodiversity and livelihoods in the Lac Télé Community Reserve, Congo Basin*", I present findings derived from field data collection in the Lac Télé Community Reserve, a seasonally flooded site in the northern Republic of Congo. Across four villages spanning swamp to *terra firma* forests, 80 semi-structured interviews, 111 structured interviews and eight focus groups were conducted to document local climate change, impacts on biophysical systems and human adaptation responses, through the knowledge of local communities. Results indicate significant climate change impacts in this site, including increasing temperatures, shifting precipitation patterns and intensified flooding, as well as associated impacts on local biodiversity, such as increased tree mortality, disrupted fish reproduction or disrupted migratory patterns in mammal species. Local communities have implemented diverse adaptation responses, e.g. changes in fishing and agricultural practices, which may exert additional anthropogenic pressures on biodiversity. This chapter highlights the value of local ecological knowledge as a complementary tool for ecological monitoring in data-deficient ecosystems and underscores the need to assess similar climate changes across other swamp forests and seasonally inundated sites.

In my third research chapter, called "*Shrinking climatic space: Implications for forest elephant conservation in the Congo Basin under climate change*", I assessed climate change impacts on the African forest elephant, a Congo Basin keystone species playing a critical role in shaping forest structure and dynamics. While forest elephants face severe pressures from illegal wildlife trade and habitat loss, climate change acts as an emerging but understudied threat. I used a bioclimatic envelope modeling (a method used to predict the suitable climatic conditions for a species based on its known occurrences and associated bioclimatic variables) and an ensemble forecasting approach (which refers to the integration of multiple models or algorithms to improve prediction reliability) to assess shifts in climatic suitability for the forest elephants under a low (SSP 245) and high-greenhouse gas emissions (SSP 585) scenarios by 2100. Given sampling biases associated with occurrence data across the species' range, I developed a two-approaches framework to estimate species presence. The first standard approach utilized occurrences obtained from the Global Biodiversity Information Facility (GBIF) and iNaturalist platforms, while the second approach employed a regular sampling of pseudo-presences within the species geographic range, as delineated by the IUCN Red List of Threatened Species. Projections reveal a consistent decline in suitable climatic conditions across datasets and scenarios, with contraction in climatic suitability in the central Congo Basin and increased fragmentation in West Africa. Critically, projections indicate that half of the current protected area network will lose climatic suitability. When accounting for future deforestation risk, the overlap between projected areas of climatic suitability and high deforestation pressure further exacerbates conservation challenges, underscoring an increasingly precarious outlook for the long-term persistence of forest elephant populations. These findings should inform conservation strategies for the forest elephant under climate change, particularly by guiding the designation of new protected areas to safeguard future climatically suitable habitats.

Overall, this PhD research underscores the value of interdisciplinary approaches in climate change and ecological science. By integrating systematic literature reviews, local ecological knowledge and ecological modeling, this thesis provides a cross-scalar perspective on the direct and indirect impacts of climate change in the Congo Basin. Findings highlight, among others, the critical role of local ecological knowledge in environmental sciences, demonstrating how community-based observations can complement remote sensing and modeling efforts in data-deficient regions. From a policy perspective, this research provides valuable insights for biodiversity conservation strategies in the Congo Basin, particularly in light of global frameworks such as the Kunming-Montreal Global Biodiversity Framework and the Paris Agreement. Ultimately, this work contributes to a broader understanding of how climate change interacts with socio-ecological systems in one of the world's most important tropical rainforests.

Résumé exécutif

S'étendant sur 2,87 millions de km² à travers six pays d'Afrique centrale (Cameroun, République centrafricaine, République démocratique du Congo, Guinée équatoriale, Gabon et République du Congo), le bassin du Congo constitue la deuxième plus grande forêt tropicale continue au monde après l'Amazonie. Abritant une diversité d'habitats (par exemple, savanes, forêts de terre ferme, marécages et forêts inondées de façon saisonnière), le bassin du Congo se classe au troisième rang mondial en termes de richesse spécifique et soutient des niveaux exceptionnels de biodiversité, incluant des espèces mégafauniques emblématiques et menacées telles que l'éléphant de forêt d'Afrique (*Loxodonta cyclotis*), le gorille des plaines de l'Ouest (*Gorilla gorilla gorilla*), le chimpanzé central (*Pan troglodytes troglodytes*) et le bonobo (*Pan paniscus*). En raison de ses vastes stocks de carbone, la région joue un rôle fondamental dans la régulation climatique mondiale, stockant environ 29 pétagrammes de carbone dans ses tourbières, en plus d'une biomasse aérienne considérable dans ses forêts.

Cependant, les forêts tropicales du bassin du Congo font face à de multiples menaces, notamment la déforestation et la dégradation forestière dues à l'agriculture à petite et grande échelle, ainsi qu'aux industries extractives telles que l'exploitation forestière, minière et pétrolière, auxquelles s'ajoute le commerce illégal de la faune sauvage. Le changement climatique devrait exacerber ces pressions, entraînant des conséquences profondes sur la biodiversité et les populations humaines du bassin du Congo, dont beaucoup dépendent des ressources forestières pour leur subsistance. Malgré son importance écologique et climatique, cette région demeure largement sous-étudiée : l'absence de suivi à long terme, les lacunes spatio-temporelles dans les données instrumentales et la rareté des études de terrain conduisent à l'exclusion fréquente du bassin du Congo des évaluations climatiques et de biodiversité aux échelles régionale et mondiale. Compte tenu des trajectoires des autres forêts tropicales d'importance mondiale face au changement climatique, il est impératif d'étudier les impacts actuels et futurs du changement climatique sur le bassin du Congo.

Afin de combler cette lacune critique, cette recherche doctorale vise à approfondir la compréhension des impacts directs et indirects du changement climatique sur la biodiversité du bassin du Congo, en adoptant une approche multi-échelle et interdisciplinaire. Les impacts directs incluent, par exemple, les modifications des aires de répartition des espèces, les altérations des cycles phénologiques ou les perturbations des réseaux trophiques, tandis que les

impacts indirects englobent les réponses d'adaptation humaine susceptibles d'amplifier les menaces existantes pesant sur la biodiversité. Cette étude repose sur trois objectifs principaux : 1) évaluer les impacts du changement climatique sur les systèmes biophysiques à différentes échelles spatiales ; 2) identifier les réponses locales d'adaptation au changement climatique et leurs effets indirects sur la biodiversité ; et 3) examiner les impacts du changement climatique sur une espèce clé de voûte, l'éléphant de forêt d'Afrique.

Le premier chapitre analytique, intitulé « *Un avenir incertain pour la biodiversité du bassin du Congo : Une revue systématique des impacts du changement climatique* », a analysé de manière systématique les impacts actuels et projetés du changement climatique sur la biodiversité à tous les niveaux organisationnels, des gènes aux écosystèmes. Les résultats révèlent des effets généralisés, notamment une vulnérabilité accrue des espèces à l'extinction, des changements de répartition géographique et une réduction de la taille corporelle des organismes, tandis que les études portant sur la génétique, la physiologie et la phénologie des espèces restent limitées. Les recherches combinant le changement climatique à d'autres facteurs de changement, tels que les modifications de l'usage des terres ou les réponses d'adaptation humaine, projettent une perspective alarmante quant à la persistance de la biodiversité du bassin du Congo. Cependant, des lacunes substantielles subsistent, en particulier concernant la dynamique des populations, la disponibilité des ressources végétales et les changements de composition à grande échelle. Cette revue souligne l'urgence de mener davantage de recherches pour combler ces déficits de connaissances.

Le deuxième chapitre analytique, « « *Nous avons vu des poissons dans les plantations de cacao » : Observations locales des impacts du changement climatique sur la biodiversité et les moyens de subsistance dans la Réserve communautaire du Lac Télé, bassin du Congo* », présente les résultats issus de données de terrain collectées dans la Réserve communautaire du Lac Télé, un site inondé de façon saisonnière situé dans le nord de la République du Congo. Dans quatre villages répartis entre forêts marécageuses et forêts de terre ferme, 80 entretiens semi-structurés, 111 entretiens structurés et huit groupes de discussion ont été réalisés afin de documenter les changements climatiques locaux, leurs impacts sur les systèmes biophysiques et les réponses d'adaptation humaine, à travers les connaissances des communautés locales. Les résultats indiquent des impacts significatifs du changement climatique dans cette région, notamment une augmentation des températures, des modifications des régimes pluviométriques et une intensification des inondations, avec des répercussions associées sur la biodiversité locale, telles que la mortalité accrue des arbres, la perturbation de la reproduction des poissons et des modifications des schémas migratoires de certaines espèces de mammifères. Les communautés locales ont mis en place diverses stratégies d'adaptation, notamment des changements dans les pratiques de pêche et d'agriculture, susceptibles d'exercer des pressions anthropiques supplémentaires sur la biodiversité. Ce chapitre met en évidence la valeur des connaissances locales comme outil complémentaire au suivi écologique dans les écosystèmes déficients en données et souligne la nécessité d'étendre ces recherches à d'autres forêts marécageuses et sites inondés saisonnièrement.

Dans le troisième chapitre, « *Contraction de l'espace climatique : Implications pour la conservation des éléphants de forêt dans le bassin du Congo sous l'effet du changement climatique* », j'ai évalué les impacts du changement climatique sur l'éléphant de forêt d'Afrique, une espèce clé de voûte jouant un rôle essentiel dans la structuration et la dynamique des forêts du bassin du Congo. Bien que les éléphants de forêt subissent de fortes pressions en raison du commerce illégal et de la perte d'habitat, le changement climatique représente une menace émergente encore peu étudiée. J'ai utilisé une modélisation de l'enveloppe bioclimatique (une méthode permettant de prédire les conditions climatiques favorables à une espèce en fonction de ses occurrences connues et des variables bioclimatiques associées) ainsi qu'une approche de prévision par ensemble (qui consiste à intégrer plusieurs algorithmes afin d'améliorer la fiabilité des prédictions) afin d'évaluer les changements de conditions climatiques favorables pour les éléphants de forêt d'ici 2100, selon un scénario à faibles émissions (SSP 245) et un scénario à fortes émissions de gaz à effet de serre (SSP 585) à l'horizon 2100. Compte tenu des biais d'échantillonnage associés aux données d'occurrence sur l'aire de répartition de l'espèce, j'ai développé deux approches pour estimer la présence des éléphants de forêt. La première, une approche standard, a utilisé les occurrences issues de la Global Biodiversity Information Facility (GBIF) et la plateforme iNaturalist. La seconde approche s'est basée sur un échantillonnage régulier de pseudo-présences au sein de l'aire géographique de l'espèce, telle que définie par la Liste rouge des espèces menacées de l'UICN. Les projections révèlent un déclin constant des conditions climatiques favorables, avec une contraction de l'adaptation climatique dans le centre du bassin du Congo et une fragmentation accrue en Afrique de l'Ouest. De manière critique, les projections indiquent que la moitié du réseau actuel d'aires protégées perdra son adéquation climatique. En tenant compte du risque futur de déforestation, le chevauchement entre les zones projetées comme climatiquement adaptées et les zones soumises à une forte pression de déforestation exacerbe davantage les défis de conservation, mettant en évidence des perspectives de plus en plus précaires pour la persistance à long terme des populations d'éléphants de forêt.

Dans l'ensemble, cette recherche doctorale met en évidence la valeur des approches interdisciplinaires en science du climat et en écologie. En intégrant des revues systématiques de la littérature, des connaissances écologiques locales et la modélisation écologique, ce travail de thèse offre une perspective multi-échelle sur les impacts directs et indirects du changement climatique dans le bassin du Congo. Les résultats soulignent, entre autres, le rôle fondamental des savoirs écologiques locaux en sciences environnementales, en démontrant comment les observations des communautés peuvent compléter la télédétection et les efforts de modélisation dans les régions où les données sont limitées. D'un point de vue politique, cette recherche fournit des éléments essentiels pour l'élaboration de stratégies de conservation de la biodiversité dans le bassin du Congo, en particulier dans le cadre des initiatives mondiales telles que le Cadre mondial de la biodiversité de Kunming-Montréal et l'Accord de Paris. En définitive, ce travail contribue à une compréhension plus large des interactions entre le changement climatique et les systèmes socio-écologiques au sein de l'une des forêts tropicales les plus importantes au monde.

Bokuse ya mokambi

Ezalaka na etando ya 2,87 milyon km², mpe etambolaka na bikólo motoba ya Afrika ya Kati (Kamerun, Republíki Santrafrika, Republíki Demokratîki ya Kongó, Guinée Équatoriale, Gabó, mpe Republíki ya Kongó), Zamba ya Kongó ezali zamba ya mibale monene koleka na mokili mobimba, nsima ya Amazonie. Zamba oyo ezali na bisika ebele ya bomoi (na ndakisa, esóbé, zamba ya mabele makasi, zamba ya mayi, to zamba oyo ebebaka na ndelo ya mbula) mpe ezali esika ya misato monene na mokili mobimba na bobángi ya banyama mpe bituka ya bomoi. Ezali mpe na banyama minene mpe libungutulu oyo ezali kokufa, lokola nzoku ya zamba (*Loxodonta cyclotis*), ebobo (*Gorilla gorilla gorilla*), sumbu (*Pan troglodytes troglodytes*) mpe bonobo (*Pan paniscus*). Banda na bobángi monene ya kaboni, esika oyo ezali na motuya mingi mpo na kobatela klima ya mokili, epai ezali kobomba 29 pétagrammes ya kaboni na bitekuteku na yango, elongo na masanga ya banzete minene oyo ezali na yango.

Kasi, zamba ya Kongó ezali kobundana na mikakatano ebele, oyo esangisi kobebisama ya zamba na bobuka zamba mpo na elanga ya bato ya mike to minene, lokola mpe bisaleli ya kobimisa biloko ya mokili (kotia mabaya, misala ya minerali mpe petroli). Kobebisama ya banyama ya zamba ezali mpe likambo ya monene. Mbongwana ya klima ezali kokóma likama ya sika, mpe ekoki kokómisa mitungisi yango makasi koleka, na bobebisami ya ekolo-pibale mpe bomoi ya bato oyo bazali kobikela na bozali ya zamba. Atako esika oyo ezali na ntina monene mpo na ekosisteme mpe klima ya mokili, etikali mosika na misala mingi ya bolukiluki. Kososolama ya mikakatano na mokili ezali na bosaleli ya maye matali Esobe ya Kongó te, mpo esika yango ezali na minoko ya bolukiluki mike mpe bozangi ba-données ya ndenge nyonso. Esengeli ete tokeba ndenge bobongwani ya klima ezali kosala na zamba ya Kongó, mpe ndenge yango ekobanda kosala na mikolo ezali koya.

Mpo na kokokisa bososoli oyo ezali kozanga, bolukiluki oyo ya PhD ezali na mokano ya kopesa mayele makasi mpo na ndenge bobongwani ya klima ezali kosala na banyama mpe bisika ya bomoi na zamba ya Kongó, na kolandela etuluku ya maye matali misala mingi ya sience. Mikakatano minene ezali misato: 1) kotalela ndenge bobongwani ya klima ezali kosala na bisika ya bomoi na ba-niveau ndenge na ndenge, 2) kotala ndenge bato bazali kolandela mbongwana ya klima, mpe ndenge oyo ekoki kobebisa banyama mpe bozindo ya zamba, 3) kotalela ndenge bobongwani ya klima ezali kosala na sombi ya zamba ya Afrika (*Loxodonta cyclotis*).

Na mokapo ya liboso ya bolukiluki, oyo ezali « Mikakatano ya lobi mpo na bomoi na Esobe ya Kongó : Lisalisi ya bolukiluki mpo na ndenge bobongwani ya klima ezali kosala na banyama », nayebisi ndakisa nyonso ya ndenge bobongwani ya klima ezali kosala. Bato mingi babeti sete ya ndenge ekosala ete banyama mingi babungisa bisika na bango, babongola bisika na bango to bakoma mikuse. Kasi, bolukiluki ebele etali genetiki, fizioloji, mpe bilembo ya bana ya banyama ezali naino moke.

Na mokapo ya mibale, oyo ezali « To moni mbisi na elanga ya cacao » : Ndenge bato bazali komona bobongwani ya klima mpe ndenge ekosali na bozali ya bomoi mpe nzete na Lac Télé, Esobe ya Kongó. Nayekolaki ndenge bobongwani ya klima ezali kosala na bozali ya bomoi na bisika ekangani na mayi. Nasalaki masolo na bato 80, nakotaki masolo 111 mpe masolo 8 ya bibongiseli mpo na kolobela ndakisa ya ndenge klima ezali kobongwana na bisika oyo. Bato batángaki ndenge mbula ebongwani, ndenge mayi ekómi koleka mpe ndenge banyama bazali kobungisa bisika na bango. Bato bazali komeka kobongola misala na bango, lokola ndenge bazali kosala elanga mpe kokanga mbisi, kasi yango ekoki kokomisa mitungisi koleka mpo na banyama ya zamba. Bolukiluki oyo ezali komonisa ntina ya maye matali mayele ya bato ya lokóta mpo na kotalela bozindo ya ekosisteme oyo ezali na ba-données moke.

Na eteni na ngai ya misato ya bolukiluki, *« Kokitisa esika ya bozali ya mabele: Bantina mpo na kobatela nzoko ya zamba na Esika ya Mbula ya Kongo liboso ya mbongwana ya klima »*, nalukaki koyeba ndenge mbongwana ya klima ezali kosala impact na nzoko ya zamba ya Afrika, oyo ezali esika ya moke ya libulamatari na Esika ya Mbula ya Kongo mpe ezali na mokumba monene na kosala forme ya molongo ya zamba mpe bomoi ya ekosisteme. Atako banyama oyo bazali kobundana makasi mpo na mipasi ya commerce ya banyama ya mabe mpe kobungisa bisika ya kofanda, mbongwana ya klima ezali kobima lokola likama ya sika, kasi ezali nanu koteyama malamu te. Nasalelaki modèle ya enveloppe bioclimatique (moyekoli moko oyo esalisaka mpo na kopesa bilembo ya bisika oyo ekozala malamu mpo na bomoi ya ekobo moko kolanda bisika bazali komonana mpe biloko ya mabele ezali kosala impact na yango). Nasalelaki mpe ndakisa ya esika ya suka ya malamu (ensemble forecasting), oyo ezalaki kokangisa banyama ya modɛlɛ ebele mpo na kobakisa bosenga ya malamu ya mayebisi. Bolukiluki na ngai esalaki botali ya kobongwana ya bisika ya malamu mpo na nzoko ya zamba na ndakisa mibale ya makambo ya ntina: mbongwana ya moke ya gaz ya makila (SSP 245) mpe mbongwana ya makasi ya gaz ya makila (SSP 585) kino na mobu 2100. Na kotalela bizaleli ya mabe na sampuli ya makambo etali bilembo ya bomoi ya nzoko na bisika na yango, nasalaki maye matali ndakisa mibale mpo na koyeba esika wapi banyama bazali. Ndakisa ya liboso, oyo ezali ya standard, esalelaki bilembo euti na Global Biodiversity Information Facility (GBIF) mpe plateforme ya iNaturaliste, mpe ndakisa ya mibale esalelaki sampuli ya bilembo ya ndenge moko (pseudo-presences) kati na esika ya nzoko kolanda carte ya IUCN Red List ya banyama bazali na likama. Makambo ezwamaki emmonisi ete bisika ya malamu mpo na nzoko ezali kokitisa mingi na bikateli nyonso, elongo na kokitisa ya bisika ya malamu kati na Esika ya Mbula ya Kongo mpe kopanzana mingi na Afrique de l'Ouest. Makambo oyo ezali kosala mopanzi monene ezali ete bisika ya kala oyo babatelaki banyama ekobungisa ndambo ya molai ya bisika ya malamu mpo na nzoko. Ntango tokotala mpe likama ya kobebisama ya zamba na mikolo ezali koya, esika oyo ekozala malamu na mabele mpo na nzoko ekozala mpe na likama ya kobebisama mingi, mpe likambo oyo ekobakisa mpasi ya kobatela banyama wana, mpe ekopesa mwa esengo moke mpo na kozala ya ntango molai ya nzoko ya zamba. Makambo oyo esengeli kokamba bibongiseli ya kobatela nzoko ya zamba liboso ya mbongwana ya klima, mingimingi na kolakisa bisika sika ya kobatelama mpo na kokoba kobatela bisika oyo ekokoka na klima ya mikolo ezali koya.

Na mobimba na yango, bolukiluki oyo emmonisi ntina ya ndenge ebele ya mayebisi na mbongwana ya klima mpe siansi ya ekolojia. Na kokangisa botali ya makomi, mayele ya ekolojia ya bato ya mboka, mpe modɛlɛ ya ekolojia, makomi oyo epesi botali ya bisika ebele mpo na impact ya mbongwana ya klima ya ntina mpe oyo ezali ndenge moko te na Esika ya Mbula ya Kongo. Makambo oyo emmonisi ete mayele ya bato ya mboka ezali ya ntina mingi na mayele ya ekolojia, na kolakisa ndenge nini botali ya bato ekoki kosalisa botali ya satellite mpe modɛlɛ na bisika oyo ezali na data mingi te. Na makambo etali mibeko, bolukiluki oyo epesi mayebisi ya ntina mpo na bibongiseli ya kobatela bomoi na Esika ya Mbula ya Kongo, mingimingi na kolandela mibeko ya mokili mobimba lokola Cadre mondial de la biodiversité de Kunming-Montréal mpe Accord de Paris. Na suka, mosala oyo ekobakisa boyebi ya ndenge nini mbongwana ya klima ezali kosangana na makambo ya bomoi mpe molongo ya bato, na esika moko ya zamba ya ntina mingi na mokili.

Chapter I
General introduction

Motivation and state of the art

Climate change and the Anthropocene

Human activities have produced transformations of the Earth system on a scale comparable to major geophysical, climatic, volcanic and even extraterrestrial processes in the form of meteorite impacts (Crutzen, 2002; Lewis, 2005). The magnitude and rapidity of anthropogenic environmental impacts have led to the advent of a new geological epoch called the Anthropocene (Rockström et al., 2009). This follows the relatively stable Holocene, which saw major developments in human societal and technological evolution over the last 12,000 years (Richerson & Boyd, 2001). The intensification of human-driven impacts on the atmospheric, biospheric and geospheric systems has been labelled the "*great acceleration*", encompassing 24 socio-economic and Earth system variables, including the exponential rise in human population, the consumption of synthetic fertilizer and freshwater, the increased concentrations of greenhouse gases such as nitrous oxide (N_2O) and methane (CH_4), the acidification of ocean, the loss of tropical forests and the degradation of the terrestrial biosphere (Steffen et al., 2015). Currently, atmospheric carbon dioxide (CO_2) concentrations have reached 425 parts per million by volume (ppmv, Mauna Loa Observatory, NOAA, 2025), at their highest levels since 2 million years (IPCC, 2023). Concomitantly, global surface temperatures have risen by 1.2°C above pre-industrial levels (Forster et al., 2024), even surpassing, for the first time, 1.5°C of warming during a 12-month period in 2024 (COPERNICUS, 2025). A prolonged overshoot - even if it stays temporary - of the 1.5°C threshold, defined by the Paris Agreement as the long-term temperature target, significantly increases the risk of triggering climate tipping elements (T. Möller et al., 2024). Tipping points are defined by the Intergovernmental Panel on Climate Change (IPCC) as "*critical thresholds in the [climate] system, that, when exceeded, can lead to a significant [often irreversible] change in the state of the system*" (IPCC, 2021, p.2876). They include the Greenland Ice Sheet, large-scale oceanic and atmospheric circulation patterns such as the Atlantic Meridional Overturning Circulation and biosphere sub-systems like the Amazon rainforest, several of them displaying early signs of transition. Even under scenarios comprising aggressive greenhouse gas emission mitigation (e.g. the Shared Socio-economic Pathways 119 to 126[1]), the rise in global temperature is projected to reach an additional 0.5°C to 1.0°C by 2100. The implementation of currently announced climate policies could lead to 3.2°C of global warming, whereas current levels of greenhouse gas emissions are consistent with a high-risk scenario of 4.4°C of warming (RCP 8.5 and SSP 585) by 2100 (IPCC, 2021).

Anthropogenic alterations of the Earth system have driven profound restructuring in biodiversity, here defined as the "*variability among living organisms from all sources, including terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part*", at local and global scales (Pörtner et al., 2021, p.248). In a joint report, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and the IPCC established that 77% of land (excluding Antarctica) and 87% of the ocean are impacted by anthropogenic activities. Out of 166,000 species assessed in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, more than 46,300 are currently classified as threatened with extinction, including 41% of amphibians, 38% of trees, 37% of sharks, rays and chimeras, 21% of reptiles, 26% of freshwater fishes and 44% of reef-forming corals (IUCN, 2024). Approximately 500,000 plant and animal species are labeled "*dead species walking*", doomed to extinction unless urgent measures are taken to mitigate the intensity of biodiversity loss drivers (IPBES, 2019). The colossal decline in biodiversity has led to a loss of 83% of wild mammal biomass: currently, only 4% of mammals on Earth are wild, while livestock and human mass amount to, respectively, 60% and 36% of remaining mammal mass (Bar-On et al., 2018). Similarly, wild birds represent 30% of total bird biomass, the remaining 70% consist of poultry. Current defaunation is consistent with extinction rates characterizing the Earth's previous five great mass extinction events (the Ordovician, Devonian, Permian, Triassic and Cretaceous events), which were triggered by various phenomena, including global cooling, volcanism and asteroid impacts. Present levels of extinction, estimated to be up to 1,000 times higher than background rates, have led to the

[1] Shared Socio-economic Pathways (SSPs) portray five alternative narratives of socio-economic developments, including sustainable development (SSP 119), middle-of-the-road development (SSP 245), regional rivalry (SSP 370), inequality (SSP 460) and fossil-fueled development (SSP 585), which correspond to different levels of global warming. Representative concentration pathways (RCPs) are a set of standardized greenhouse gas (GHG) concentration trajectories used in climate modeling to project possible future climate scenarios based on different levels of radiative forcing (including RCP 1.9, RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5, Riahi et al., 2017).

designation of the present biodiversity crisis as the "*sixth mass extinction*" (Barnosky et al., 2011).

While land-use change, the overexploitation of natural resources, pollution and the introduction of invasive alien species are the primary threats to biodiversity, climate change is increasingly recognized as a leading cause of biodiversity loss (Pacifici et al., 2015). Scientific consensus highlights climate change effects on all biodiversity organizational levels, from genes to ecosystems, and across most ecological processes fundamental to ecosystem functioning (Bellard et al., 2012; Scheffers et al., 2016). Worldwide, documented impacts of climate change on biodiversity include shifts in species distributional range (Milad et al., 2011), physiological stress (Weiskopf et al., 2020), shifted migratory patterns and modified phenological timing (Gezon et al., 2018). A variety of other impacts, including effects on genetic variation, intra and interspecific interactions or community structure, are likely occurring but remain undocumented (Scheffers et al., 2016). Synergistic interactions between multiple drivers of change, including land-use and climate change, have the potential to induce substantial shifts in ecosystem states (Mantyka-Pringle et al., 2015). Habitat fragmentation, for instance, can impede species' ability to track shifting climatic conditions. As global temperatures continue to rise, the emergence of novel climate regimes is anticipated, presenting conditions under which species' adaptive capacities remain uncertain (Trisos et al., 2020). This may result in significant and abrupt disruptions to species assemblages, with profound implications for ecosystem stability and biodiversity persistence.

Human adaptation to climate change and indirect impacts on biodiversity

The accelerating impacts of climate change threaten not only biological diversity but also cultural diversity, both of which are deeply interwoven within the concept of biocultural diversity - the dynamic interrelationship between ecosystems, species and human cultures that co-evolved with nature (Reyes-García et al., 2023a). Climate change is already exerting profound effects on human societies, with escalating risks to livelihoods and well-being, particularly for Indigenous Peoples and Local Communities (IP&LC), whose ways of life are inextricably linked to their environments (Jarillo & Crivelli, 2024). IP&LC are described as "*individuals and communities who are, on the one hand, self-identified as Indigenous and, on the other hand, are members of local communities that maintain intergenerational connection to place and nature through livelihood, cultural identity and worldviews, institutions and ecological knowledge*" (IPBES, 2019, cited by McElwee et al., 2020, p.2). The livelihoods of an estimated 370 million IP&LC individuals are at heightened risk due to extreme weather events of increased severity and frequency, including droughts, floods and heatwaves (Filho et al., 2021). Climate-sensitive sectors, including agriculture, fisheries, forestry and tourism, are expected to face significant economic losses, potentially undermining decades of socio-economic progress in developing regions (Ford et al., 2015). Projections suggest that, between 2030 and 2050, climate change could contribute to an additional 250,000 deaths per year due to malnutrition, heat stress or vector-borne diseases such as malaria or dengue (Pörtner et al., 2021).

The implementation of adaptation strategies, defined by the IPCC as "*the process of adjustment to actual or expected climate and its effects, in order to moderate harm*", is deemed critical for mitigating climate-induced risks (IPCC, 2023, p.2898). Within the literature, most existing research consists of descriptive studies documenting the diversity of adaptation responses globally. For example, in high-income countries, adaptation efforts are often centered on policy, regulation and infrastructure development (Berrang-Ford et al., 2021). In Small Island States, costal flood management programs are the most commonly reported responses. In Asia and Africa, adaptation mostly takes place at the household level, and farmers have increasingly adopted drought-resistant crops, diversified income sources (e.g., labor migration) and shifted livestock management strategies in response to erratic rainfall patterns (Berrang-Ford et al., 2015). Among IP&LC groups, a diversity of responses tied with natural resource-dependent livelihoods is observed, such as changes in grazing locations, the use of water conservation techniques and the adoption of improved fishing methods (Schlingmann et al., 2021). However, regional disparities in research persist, with adaptation responses disproportionately documented in North America, Europe, Southeast Asia and portions of anglophone Africa. In large parts of the world, including Central Africa, the scientific understanding of how and where adaptation occurs remains largely incomplete (Ford et al., 2015).

Another considerable oversight in the current literature is the limited consideration of the impacts of human adaptation responses on biodiversity. A slowly emerging field of research strive to identify what are called the "*indirect impacts of climate change on biodiversity*", which arise from human adaptation exacerbating existing conservation threats (Segan et al., 2015; Watson & Segan, 2013). For instance, in Ghana, declining fish stocks have led to increased bushmeat hunting, intensifying anthropogenic pressure on terrestrial wildlife populations (Brashares et al., 2004). Quantitative assessments of the indirect impacts of climate change on species remain scarce. One of the few documented cases involves the long-tailed ground-roller (*Uratelornis chimaera*) in Madagascar. While climate models initially suggested no direct habitat loss for this species, further analysis revealed that local communities, facing declining agricultural yields, were expanding farmland into the ground-roller's range, thereby increasing its extinction risk (Segan et al., 2015). Similarly, a re-evaluation of the climate vulnerability of range-restricted bird species resulted in the risk status of 164 species shifting from "*low*" to "*high*" when human adaptation responses were incorporated into the assessment (Segan et al., 2015). These findings underscore the importance of integrating human behavioral responses into conservation planning, as the interplay between direct and indirect climate threats may generate unforeseen biodiversity risks, potentially compromising conservation progress achieved to date (Dawson et al., 2011). Current adaptation literature rarely accounts for indirect climate change impacts on biodiversity. Adaptation measures that unintentionally exacerbate biodiversity risk should be classified as maladaptive, as defined by the IPCC: "*actions that may lead to increased risk of adverse climate-related outcomes* [...]*, increased or shifted vulnerability*" (IPCC, 2023, p.2915). Without such integrated approach, maladaptive strategies may inadvertently undermine both human adaptation to climate change and biodiversity conservation objectives.

The global significance of Congo Basin rainforests

Tropical rainforest ecosystems, as defined by the United Nations Food and Agriculture Organization (FAO), are forests with a tree canopy cover exceeding 10%, a height surpassing five meters and an area greater than 0.5 hectares, occurring between the Tropics of Cancer and Capricorn (FAO, 2020). Tropical rainforests are widely recognized as global reservoirs of biodiversity (Lewis, 2005), hosting an estimated two-thirds of all known species (Dirzo & Raven, 2003) and harboring 18 of the world's 25 recognized biodiversity hotspots (Myers et al., 2000). Beyond their biological significance, tropical forests account for approximately one-third of Earth's terrestrial gross primary productivity (Bonan, 2008) and store half of the planet's carbon sequestered in terrestrial vegetation (Hubau et al., 2020). Additionally, they sustain the livelihoods of 1.6 billion people who depend on forest resources for food, medicine and income (FAO, 2020). Despite their undisputable ecological value, tropical rainforests remain notably understudied, leaving fundamental questions open, for example: what proportion of tropical biodiversity remains undocumented? How will tropical ecosystems respond to global changes? What are potential ecological tipping points in tropical rainforest ecosystems under the combined pressures of climate change and deforestation?

This underrepresentation is particularly pronounced in the Central African Congo Basin. With an extent of 2.87 million km^2, the Congo Basin constitutes approximately 30% of global tropical forests and the world's second-largest block of continuous rainforest (Malhi et al., 2013). The hydrographic basin of the Congo river covers a vast drainage area, spanning 3.7 million km^2 across seven countries (Karam et al., 2023), but the denomination "*Congo Basin*" is used to designate six countries characterized by their substantial forest cover: Cameroon, the Central African Republic, the Democratic Republic of the Congo (DRC), Equatorial Guinea, Gabon and the Republic of Congo (Devers et al., 2006). The Congo Basin is home to approximately 139 million people, with significant demographic disparities - from 2.3 million in Gabon to over 95.3 million in the DRC (UNDP, 2022). In 2022, countries in the region ranked from 123 to 191 on the Human Development Index (out of 193 countries), with life expectancy ranging from 54.5 to 65.7 years, mean years of schooling between 4 and 9.6 years, and per capita income from \$869 to \$11,194. In 2023, over 31% of the population lived on less than \$2.15 per day (UNDP, 2022).

The Congo Basin is the subject of much less public and scientific scrutiny than the Amazon Basin (which has an extent of approximately 8 million km^2, Terborgh et al., 2016), but is a key biodiversity center, serving as a major carbon sink (Lewis et al., 2013) and an important regulator of regional and global climate systems (Bonan, 2008). Its forests notably supply essential moisture that sustains rainfall in the Sahel and the Ethiopian highlands (Trigg & Tshimanga, 2020). While the Congo Basin shares common features with other tropical forest ecosystems, such as a high species diversity, a closed canopy, a dense vegetation and several strata of forest structure, it also exhibits key structural differences. It is notably situated at higher elevation, ranging from 300 to 1,000 meters above sea level (Malhi & Wright, 2004), experiences colder temperatures (~1.1°C cooler than Amazon forests, Hubau et al. (2020) and contain larger trees (Lewis et al., 2013) with higher wood mass density (Terborgh et al., 2016). Extending from the Albertine Rift mountains to the Atlantic ocean, its topography is characterized by a bowl-shaped depression known as the Cuvette centrale (Bola et al., 2022). This lower-altitude terrain (with an altitude ranging between 275 to 460 meters above sea level) evolved to its current form during the Mesozoic (252-66 million years before present, B.P.) and Cenozoic periods (66 million years B.P. to present, Kadima et al., 2011). While the region's hydrology remains poorly understood, the Congo river, originating in the southeastern DRC, is the second-longest river in Africa (4,700 km) and forms a vast water catchment structured around four main tributarie, the Oubangui, Sangha, Kasai and Lualaba rivers, each with its own drainage system. A substantial human population - about 100 million people - is dependent on Congo river resources for navigation (with 25,000 km of navigable river routes), drinking water, irrigation and access to broader ecosystem services within the Congo Basin (Bates et al., 2024). Seasonal floods are a distinctive feature of Congo river riparian habitats, acting as a key constrain for ecosystem and species distribution (Nowak et al., 2019), and influencing biotic composition, nutrient advection (Bola et al., 2022) and peatland carbon emissions (Biddulph et al., 2021). The scientific understanding of flood seasonality and their spatial and temporal variations also remains limited.

As one of the three core convective regions - alongside the Maritime continent of the tropical West Pacific and Eastern Indian oceans and the Amazon Basin - the Congo Basin exhibits distinctive climatic characteristics (Washington et al., 2013). Mean temperatures remain mostly stable throughout the years, ranging between 26-28°C (Malhi & Wright, 2004). The region's climate is controlled by a bimodal rainfall pattern, with dry season length varying along both latitudinal (distance from the Equator) and longitudinal (east-west) gradients (Bush et al., 2020a). The annual precipitation averages 1500–2000 mm yr^{-1} in the central Congo Basin, with higher levels of 2500-3000 mm yr^{-1} in the Atlantic coastal region, comparable to those recorded in the Amazon Basin (Asefi-Najafabady & Saatchi, 2013). Rainfall seasonality, while still not fully understood, has been showed to be primarily influenced by Intertropical Convergence Zone (ITCZ) dynamics, a low-pressure belt associated with high clouds cover and high precipitation along the Equator. Additionally, associations between seasonal rainfall variability and large-scale oceanic and atmospheric patterns linked with increased sea surface temperature - notably the El Niño Southern Oscillation (ENSO) - have also been demonstrated (Nicholson et al., 2018). Seasonal rainfall patterns drive spatial and temporal variation in flood dynamics across the Congo Basin (Bola et al., 2022).

The Congo Basin represents a critical component of the global carbon cycle, owing to its exceptional carbon sequestration capacity. Congo Basin rainforests are characterized by remarkably high levels of above-ground biomass (AGB), averaging 429 Mg dry mass ha^{-1}, significantly exceeding Amazon AGB estimates of 289 Mg dry mass ha^{-1} (Lewis et al., 2013). Unlike the Amazon Basin, where carbon sequestration efficiency has declined over recent decades, the carbon sink capacity of live AGB in African tropical forests has remained stable up to 2015. The relatively greater carbon accumulation in African forests is attributed to slower rates of warming, fewer and less severe drought events, lower forest sensitivity to droughts and overall cooler temperatures (Hubau et al., 2020). Additionally, the largest tropical peatland complex in the world was recently described in the Cuvette centrale, with an estimated extent of 167,600 km^2 (Dargie et al., 2017). Storing 29 petagrams of carbon, this vast expense of near-continuous peatlands is recognized as one of the most carbon-rich ecosystems on Earth, storing the equivalent of 15 years of U.S. greenhouse gas emissions, or the total above-ground forest biomass within the Congo Basin (Sonwa et al., 2022). These peatlands began forming around 10,500 years B.P. and have actively sequestered carbon throughout the Holocene, maintaining a high degree of integrity to this day.

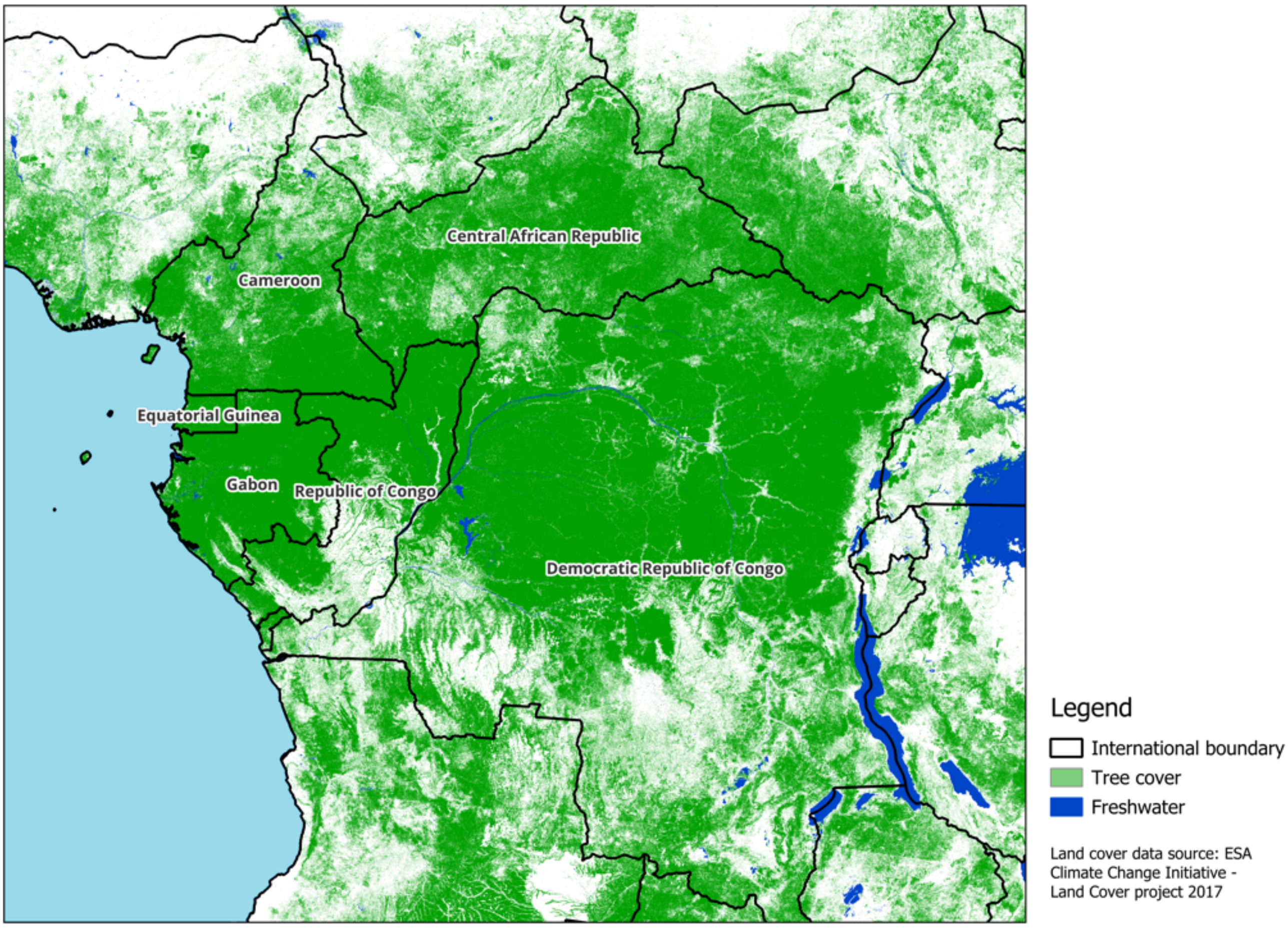

Figure 1: Forest cover in Congo Basin countries. Data source: ESA.

Congo Basin biological diversity

In the Congo Basin, large-scale, connected rainforests stretches continue to sustain ecological processes. Based on dominant tree taxa, Réjou-Méchain et al. (2021) identified ten major forest types across the Congo Basin, reflecting high level of floristic and structural heterogeneity: the Atlantic highland evergreen, Atlantic coastal evergreen, Atlantic island evergreen, margin semideciduous, evergreen semideciduous on sandstone, semideciduous, central evergreen, mixed evergreen, degraded semideciduous and semideciduous evergreen transition forests. Unlike the Amazon and Southeast Asia, where soil properties predominantly govern tree community structure, floristic assemblage in the Congo Basin are primarily shaped by the climate. In addition to this classification (and among the many that exists), permanently flooded swamp forests (where flooding exceed 9 months per year), periodically flooded swamp forests (with 4-9 months of flooding), riparian forests, grasslands and mangroves must also be considered (Dalimier et al., 2021). Largely located in the center Congo Basin, swamp forest ecosystems include hardwood swamp forests, dominated by species such as *Uapaca* spp., *Carapa procera,* and *Xylopia rubescens*, and palm-dominated swamps, characterized by the occurrence of *Raphia laurentii* (Sonwa et al., 2022). Notably, the ecological integrity of Congo Basin rainforests is tightly linked to megafaunal interactions, with up to 79% of large tree species estimated to rely on the African forest elephant (*Loxodonta cyclotis)* for seed dispersal (Beaune et al., 2013).

Often described by their exceptionally high levels of biological diversity, Congo Basin forests harbor an estimate of 10,000 plants, 400 mammal, 1,000 bird, 700 fish and 280 reptile species, alongside a variety of insect species (Yuh et al., 2024). Main floral families include *Bambusoideae*, *Araceae*, *Araliaceae*, *Flacourtiaceae* and *Marantaceae* (Yuh et al., 2024), with plant endemism gauged at 80% (Eba'a Atyi et al., 2022). Main centers of species richness identified include Mount Cameroon, the Cameroon highlands or the Kivu center, coinciding with areas of increased rainfall or altitudinal variation (Plana, 2004). The Congo Basin is home to a unique assemblage of megafaunal species, including the forest elephant, hippopotamus (*Hippopotamus amphibius*), African buffalo (*Syncerus caffer*)*,* okapi (*Okapia johnstoni*) and sitatunga (*Tragelaphus spekei*). It is the only tropical region hosting four great ape species, such as the western lowland gorilla (*Gorilla gorilla gorilla*), Cross river gorilla (*Gorilla gorilla diehli*), central chimpanzee (*Pan troglodytes troglodytes*) and bonobo (*Pan paniscus*), alongside a large primate community, including the Allen's swamp monkey (*Allenopithecus nigroviridis*), the cercocebe *Cercocebus agilis*, the Brazza cercopithecus (*Cercopithecus neglectus*) or the guéréza colobus (*Colobus guereza*). Three African crocodile species are present, including the Nile crocodile (*Crocodylus niloticus*)*,* the false gharial (*Crocodylus cataphractus*) and the dwarf crocodile (*Osteo laemus tetraspis*, IUCN, 2024). Freswater habitats support a diverse assemblage of aquatic species, including numerous endemic fish, crabs and mollusks (Inogwabini & Lingopa, 2013). The region also harbors high avian endemism, with species such as the Congo peafowl (*Afropavo congensis*), the anhinga *Anhinga rufa* and the purple heron *Ardea purpurea* (Fishpool & Evans, 2001). From 2013 to 2023, 742 Congo Basin animal and plants species were described as new to science, including 14 new orchid species (from the *Angraecum, Bulbophyllum, Cyrtorchis* or *Polystachya* genera), the firefly *Afrodiaphanes pulcher*, electric fish *Petrocephalus arnegardi*, the Central African slender-snouted crocodile *(Mecistops leptorhynchus)* and the Mongo hairy bush viper (*Atheris mongoensis*, WWF, 2024). However, biodiversity inventories in the Congo Basin remain incomplete, with significant knowledge gaps across most taxonomic groups, and the ecological dynamics of its rainforests is largely under-documented (Chifundera, 2019; Diamond & Hamilton, 1980; Sonwa et al., 2022).

Congo Basin rainforests have undergone large-scale ecological shifts in the past, likely driven by climate change. Over the last 10 million years, the region has experienced cycles of forest expansion and contraction (Brncic et al., 2006). Extreme shifts in forest cover, sometimes resulting in permanent forest loss, are thought to be linked to rainfall variability, potentially driven by fluctuations in sea surface temperature. One of the most significant forest regression events occurred between 3000 and 2000 years B.P. during the Late Holocene, attributed to a weakening of the African monsoon (Oslisly et al., 2013). Pollen records from this period indicate alternating dominance of humid forest tree taxa and light-demanding pioneer and herbaceous species, characteristic of degraded forests and savannas (Ngomanda et al., 2009). According to the rainforest refugia theory, severe climatic fluctuations led to the fragmentation of lowland rainforests into isolated refugia, where forest-obligate species persisted (Plana, 2004). These historical refugia have had lasting effects on species distributions, influencing present-day biodiversity patterns in the Congo Basin, along with the Congo river, which acts as a major distributional barrier for many vertebrates (van de Perre et al., 2020).

Congo Basin cultural diversity

The Congo Basin rainforests are not only ecologically diverse, but also encompass a remarkable cultural diversity. Far from a pristine "*Eden*" barren of anthropogenic activities (Nsah, 2023), the Congo Basin has been inhabited since prehistoric times (Boyette et al., 2022). Archeological evidence suggests the presence of modern *Homo sapiens* as early as 40,000 B.P., with early foragers adapting to the region's complex mosaic of micro-ecosystems and variation in natural resource distribution. By 2000-4000 B.P., technological innovations such as pottery, metallurgy and fire-based practices associated with palm oil (*Elaeis guineensis*) cultivation had emerged, likely contributing to forest shifts (Brncic et al., 2006). The combined effects of early anthropogenic activities and past climatic shifts may have left enduring footprints on modern forest composition (Oslisly et al., 2013). Evidence suggests that foraging cultures existed at least 20,000 B.P., while savanna-dwelling Bantu-speaking populations migrated towards the forest periphery around 5000 B.P., marking significant cultural and ecological transitions (Fa et al., 2016).

Today, the Congo Basin is home to at least 250 different ethnic groups, including the Kongo, Luba, Beti-Pahuin, Teke, Baka, Aka, Mbuti, Mbendjele or Twa, among others (Boyette et al., 2022). Such ethnic diversity mirrors the linguistic richness of the region: for instance, the DRC is one of the most linguistically diverse countries in the world, with over 200 spoken languages, including Lingala, Swahili, Mongo, Ngbandi, Tchokwé or Kikongo. Cameroon is also home to 273 living indigenous languages such as Fulfulde, Duala, Ewondo, Basaa and Maka (Dimmendaal, 2008). Today, an estimated 100 million people from IP&LC groups directly depend on forest resources for their sustenance, housing, health and well-being, as well as cultural and spiritual practices (Eba'a Atyi et al., 2022). Their subsistence activities are diverse and vary according to ethnic groups, involving fishing, hunting (targeting species such as, for example, as the buffalo, sitatunga, duiker and porcupine), small-scale agriculture (including slash-and-burn cultivation and fallow cycles) and the gathering of non-timber forest products (NTFP) such as roots (e.g. wild yams of *Dioscorea* spp.), fruits (e.g. *Irvingiaceae* spp.), mushrooms (e.g. *Marasmius* spp.), caterpillars (e.g. *Imbrasia truncata*) or rattan (e.g. *Laccosperma secundiflorum*, (Eba'a Atyi et al., 2022; Numbi et al., 2024). Thanks to their direct dependence on natural resources and their long-term interactions with the land, Congo Basin IP&LC groups maintain a wealth of specialized knowledge about their forest environment, referred to as local ecological knowledge. However, much of this knowledge remains insufficiently documented.

Threats to biodiversity in the Congo Basin

Deforestation and forest degradation

Congo Basin rainforests are undergoing profound transformations driven by both historical and contemporary anthropogenic pressures (Reiche et al., 2021). Historically, Congo Basin rainforests have exhibited relatively modest deforestation rates (0.28% yr^{-1} for 1990-2000 and 0.14% yr^{-1} for 2000–2010), significantly lower than those observed in other tropical forested areas of significance (Mayaux et al., 2013). For example, deforestation estimates are three time higher in West Africa, and 17% of forest cover has been lost in the last 50 years in the Amazon (Beuchle, 2023; Mayaux et al., 2013). However, recent trends indicate accelerating forest loss - with approximately 1 million hectares cleared annually, exhibiting stark regional disparities

(Yuh et al., 2024). Gabon has largely maintained forest cover, with only 1.3% of primary rainforest loss since 2000, while the DRC and Cameroon rank among the highest deforestation contributors globally (Karsenty, 2020). Since 2014, deforestation in the DRC has increased sharply to approximately 450,000 hectares of primary rainforest loss yr^{-1}, positioning it as the second-largest contributor to global tropical forest loss after Brazil. Between 2000 and 2021, the DRC lost 5.6% of its primary forest, followed by Cameroon (4.2%) and Equatorial Guinea (2.9%, WRI, 2025). Less than 70% of Congo Basin rainforest remains fully intact, a decline from 78% in 2000 (Shapiro et al., 2021). Under a business-as-usual deforestation scenario, extensive forest fragmentation is projected in the DRC by 2100, isolating smaller patches from a relatively intact rainforest block in the western Congo Basin (Vieilledent et al., 2023).

The relative importance of deforestation drivers remains a subject of ongoing debate due to regional variability in forest disturbance, shaped by economic, political and demographic factors (Tyukavina et al., 2018). An array of studies identifies small-scale agriculture as a primary driver of forest loss, accounting for approximately 84% of forest disturbance between 2015 and 2020 (Karsenty, 2020; Mayaux et al., 2013; Molinario et al., 2020; Shapiro et al., 2023; Tyukavina et al., 2018). Traditional slash-and-burn practices have resulted in a shifting mosaic of subsistence plots, fallow lands and secondary forests, collectively termed the "*rural complex*" (Molinario et al., 2020). Recent studies have also described the emergence of "*perforations*", where agricultural expansion impinges from rural complexes into primary forests (Molinario et al., 2020). Deforestation intensifies in areas exceeding 8.5 people per km^2 (Ernst et al., 2010; Mayaux et al., 2013), with primary forest clearing by smallholders doubling between 2000 and 2014, paralleling population growth from 70 million in 1990 to 181 million in 2020 (Tyukavina et al., 2018). Over 50-70% of the population is rural, relying on shifting cultivation, firewood, charcoal and NTFPs, driving shorter fallow cycles and agricultural expansion (Yuh et al., 2024).

Industrial-scale activities, including logging, mining, oil, and infrastructure development, further accelerate Congo Basin deforestation (Shapiro et al., 2021). Logging is the second-largest driver of forest disturbance, accounting for approximately 10% of overall deforestation, reaching 60% in Gabon (Tyukavina et al., 2018). Rising global demand for strategic minerals – such as copper, cobalt, titanium, coltan or manganese - has further intensified deforestation pressure, with extractive industry (e.g. oil, gas or mining) concessions often overlapping with protected areas (Megevand et al., 2013; Schwartz et al., 2012). Road expansion amplifies these impacts by increasing access to remote forests: between 2003 and 2019, Congo Basin road networks expanded by 61%, from 143,700 to 230,800 km (Kleinschroth et al., 2019). Road development is extensive in *terra firma* forests under logging concessions, while Cuvette centrale wetlands remain mostly road-free, but increasingly encircled. Accurately assessing land-cover change in the Congo Basin requires better assessments of the complex interplay of deforestation drivers, yet interactions between socio-economic pressures, biophysical disturbances and climate change remain poorly documented (Geist & Lambin, 2001; Yuh et al., 2024).

Illegal wildlife trade

In many parts of the Congo Basin, large decline in wildlife have led to local extirpation, with cascading effects across multiple trophic levels and disturbance of important ecological processes such as seed dispersal, herbivory and predator-prey dynamics (Abernethy et al., 2016; Beaune et al., 2013). The loss of large-bodied herbivores, in particular, has severe consequences for forest regeneration, as many tree species rely on megafauna for effective seed dispersal and germination (Beaune et al., 2013). Among the severely affected species, the forest elephant has suffered a 62% decline, having been extirpated from 95% of its historical range in countries such as the DRC (IUCN, 2024). African great ape species have all also undergone significant population losses due to habitat loss, poaching and disease (Strindberg et al., 2018). Even within protected areas, large mammal populations have experiencing steep declines (Craigie et al., 2010; Estrada et al., 2018). While deforestation is readily quantifiable through remote sensing, defaunation remains harder to assess, despite its equally profound impact on forest structure and functional integrity (Abernethy et al., 2016).

Hunting for wild meat is a major driver of wildlife decline in the region, targeting a broad spectrum of species, ranging from large mammals to smaller taxa, including porcupines, pangolins, bats, turtles and birds (Ingram et al., 2025). While subsistence hunting is critical to rural food security, providing a primary protein source (Fa et al., 2003, 2015), increasing demand from expanding urban populations has driven the commercialization of wild meat (Abernethy et al., 2016). The circulation of advanced hunting technologies, such as firearms or wire snares, has further increased hunting efficiency (Dobson et al., 2019). Additionally, commercial hunting for high-value wildlife products, including ivory, is frequently carried out by specialized hunters operating within complex webs of suppliers and traders, linked with national and international illegal trade networks (Abernethy et al., 2013). Current extraction rates could lead to severe decline in wildlife populations and protein shortages by 2050 (Fa et al., 2003).

Political instability and armed conflicts further exacerbate defaunation by facilitating poaching, illegal wildlife trade and resource exploitation (Butsic et al., 2015). The DRC, for example, has seen a sharp increase in the circulation of weapons and ammunitions as a result of the heightened political instability that intensified during its first (1996-1997) and second (1998-2003) civil wars (Nackoney et al., 2014). Conflict periods were linked with increased hunting pressure, as armed groups and displaced communities turned to wildlife for subsistence and trade (Draulans & Van Krunkelsven, 2002). For instance, as a result of the conflicts, forest elephant densities declined by 50% in the Okapi Faunal Reserve (Beyers et al., 2011) and more than half of the gorilla population was lost to poaching in the Kahuzi-Biega National Park (Yamagiwa, 2003, cited by Funk et al., 2022).

Beyond political instability, the Congo Basin remains critically underfunded in terms of conservation financing. The DRC, which harbors some of the largest remaining populations of Afrotropical megafauna, ranks among the lowest globally in terms of biodiversity investment (Lindsey et al., 2017). Weak governance, inadequate financial support and ineffective law enforcement are also cited as contributors to wildlife decline (Beyers et al., 2011; Wilkie et al., 2001).

Uncertainty in the Congo Basin

Despite their global significance, Congo Basin rainforests suffer from a strong research deficit, fueled by the absence of long-term records and numerous temporal and spatial gaps in instrumental measurements. The data paucity has historical roots. The earliest climate and hydrological records were established during the colonial period in the first half of the 20th century, when the region was divided between Belgium (which ruled over the present DRC until its independence), France (which colonies included the Central African Republic, French Cameroon, Gabon and the Republic of Congo) and Spain (ruling over Equatorial Guinea, Bernault, 2021). Following independence from 1960-1968, archival and research activities remained geographically fragmented, with many records stored in Western institutions, including the Institut de Recherche pour le Développement (IRD, formerly ORSTOM), the Belgian Royal Academy for Overseas Sciences and the Royal Museum for Central Africa. Since the 1980s, the number of operational weather and hydrological stations has progressively declined, to the point that the Congo Basin is nowadays one of the least gauged regions globally (Washington et al., 2013). As a result, the Congo Basin is regularly omitted from regional or global-scale analyses: in 2021, Central Africa was one of only two regions globally where insufficient data prevented the IPCC from assessing historical trends in extreme temperatures (White et al., 2021).

The reliance on satellite-derived datasets has somewhat mitigated this observational gap. However, the limited density of ground-based stations severely constrains the validation and calibration of gridded observational products, introducing significant uncertainties (Washington et al., 2013). Additionally, the reliability of remote sensing data in the Congo Basin can be compromised by persistent cloud cover, which obstructs optical satellite imagery, or by the dense forest canopy, which limits the penetration of microwave and LiDAR signals used for vegetation and topographic assessments (Kashongwe et al., 2020). In rainfall datasets, there are fundamental discrepancies in assessments of both spatial distribution and total volume of regional precipitation, with estimates differing by an order of magnitude.

The comparison with the state of research in other tropical rainforests is striking. Until the mid-20th century, the hydrology and climate of the Congo Basin were better characterized than those of the Amazon (Bates et al., 2024). However, considerable investments in Amazon research, exemplified by the Large-Scale Biosphere-Atmosphere Experiment (LBA) program, a decade-long, $100-million effort which included regional-scale field and remote sensing data collection campaigns across the fields of climatology, hydrology, ecology and biogeochemistry, have positioned the Amazon as the most extensively monitored tropical rainforest ecosystem (Lahsen & Nobre, 2007; White et al., 2021). In contrast, research efforts in the Congo Basin remain hindered by multiple challenges, including its vast geographic extent, chronic underfunding, logistical constraints and political instability, all of which continue to limit the advancement of scientific knowledge on the region's ecosystems (Bola et al., 2022).

Methodological approach and scientific rationale

Considering the ubiquitous nature of climate change, the magnitude of its effects on biological systems and the critical role of the Congo Basin rainforests as a fundamental component of the Earth's system, characterizing how these ecosystems are affected by ongoing global warming is an urgent scientific endeavor. However, as discussed in the previous section, research advancements are significantly impeded by substantial scientific uncertainties and a pervasive lack of empirical data. The uncertainty surrounding climate change impacts in the Congo Basin is driven by four major knowledge gaps: the severe deficiency in meteorological data, which limits accurate climate modeling; the limited understanding of how climate change affects culture and livelihoods in the region; the lack of comprehensive research on human adaptation strategies; and the unknown consequences of these adaptive responses on biodiversity.

In this context, we propose that local ecological knowledge can serve as a pivotal resource, offering valuable insights into complex and interconnected environmental changes associated with climate change and biodiversity loss. We define here local ecological knowledge as the "*cumulative body of knowledge, practice and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment*" (Berkes et al., 2000, p.1252). The recognition of IP&LCs as environmental custodians has gained increasing prominence, including within major policy frameworks such as the IPBES and IPCC (Fa et al., 2020; McElwee et al., 2020). The critical role of IP&LC knowledge in biodiversity conservation has been acknowledged since the Convention on Biological Diversity (CBD) established during the 1992 Rio Earth Summit, particularly under Article 8(j), which mandates the respect, preservation and maintenance of traditional knowledge relevant for the conservation and sustainable use of biological diversity (CDB, 1992). Local ecological knowledge systems are deeply rooted in IP&LCs' immediate reliance on natural resources and their longstanding interactions with the biotic and abiotic components of their landscapes, enabling them to detect shifts in weather patterns, climate and ecological processes critical to their livelihoods (Reyes-García et al., 2023a). In this regard, the Local Indicators of Climate Change Impacts (LICCI) project has played a fundamental role in documenting IP&LC observations of climate change impacts and adaptation responses (Reyes-García et al., 2023b). Research within the LICCI framework has demonstrated that IP&LC knowledge frequently aligns with, complements, or corroborates instrumental climate measurements, while other studies exemplified its scientific value for monitoring ecological dynamics. For example, Fernández-Llamazares et al. (2017) documented a strong correlation between Indigenous observations and meteorological station data over a 50-year period in the Bolivian Amazon, while Early-Capistrán et al. (2020) reconstructed long-term abundance data for the East Pacific green turtle (*Chelonia mydas*) based on traditional fisher knowledge. Despite its growing recognition, local ecological knowledge remains insufficiently documented across many regions, including Central Africa, limiting its integration into scientific and policy efforts linked with climate change mitigation, climate change adaptation and biodiversity conservation. Furthermore, IP&LC themselves are increasingly vulnerable to the environmental crises, potentially undermining their ability to sustain local ecological knowledge systems and resource management practices (Sheil et al., 2003).

In parallel, ecological modeling has emerged as a critical tool for addressing data deficiencies and improving predictions of ecological changes. In a context of rapid global changes, the ability to generate timely insights into the future state of natural systems has become an indispensable aspect of ecological research. Ecological models, which employ mathematical representations of real-world processes, facilitate a better understanding of ecological drivers and their influence on observed outcomes. They offer a mean to test hypotheses that would be logistically, politically or methodologically impractical to evaluate through field studies, supporting the prioritization of empirical data collection efforts and facilitating the formulation of predictions about ecological dynamics (Breckling et al., 2011; Evans, 2012; Leland et al., 2000). A rapidly advancing branch of ecological modeling involves species distribution models, an increasingly used instrument to predict the effects of environmental change on species distributions, by identifying the relationship between species occurrence and ecological predictors.

At the intersection of local ecological knowledge and ecology, the methodological framework developed for this PhD research is firmly embedded within an interdisciplinary setting, integrating approaches from conservation biology, ethnography and ecological modeling. This integrative strategy seeks to leverage multiple sources of knowledge to advance the understanding of how climate change is reshaping biodiversity patterns in the Congo Basin, a data-deficient region. While the primary focus of this thesis is on the impacts of climate change on biodiversity in the Congo Basin, it situates these dynamics within the broader context of global environmental changes, recognizing the interplay of multiple anthropogenic drivers shaping ecosystems at regional and global scales.

Thesis structure and objectives

The aim of this PhD research study is to deepen the understanding, in a global change context, of climate direct and indirect impacts on biodiversity in the Congo Basin, adopting a multi-scalar and an interdisciplinary approach. It is based on the following objectives:

1. Assess climate change impacts on biophysical systems in the Congo Basin across multiple spatial scales (Chapters II, III and IV);
2. Identify adaptive strategies adopted by local communities in response to global change impacts on their livelihoods, and associated indirect impacts of climate change on biodiversity (Chapter III);

3. Evaluate climate change impacts on a keystone species, the African forest elephant (*Loxodonta cyclotis*, Chapter IV).

This thesis is structured into several chapters (Chapters II to IV), which employ a cross-scalar approach. Chapter II begins which a regional-scale investigation. Chapter III then narrows the focus to a local-scale analysis, while examining climate change impacts on biodiversity at the community level. Lastly, Chapter III provides a species-specific evaluation, expanding back to a regional perspective (Chapter IV).

Chapter II: Uncertain future for Congo Basin biodiversity: A systematic review of climate change impacts

My research started with an outlook at the regional level. In my first chapter, I obtained an understanding of the state of the art associated with climate change impacts in the Congo Basin. Through a literature review, I systematically outlined documented effects of climate change on Congo Basin biodiversity, whether currently observed and projected into the future, across all biodiversity organizational levels (from genes to ecosystems). This synthesis provided a comprehensive overview of existing research clusters while highlighting critical knowledge gaps that persist in the scientific literature.

Chapter III: "We saw fish in the cocoa farm": Local observations of the impacts of climate change on biodiversity and livelihoods in the Lac Télé Community Reserve, Congo Basin

Building on this regional assessment, I then examined climate change impacts at a local scale. In my second chapter, I examined the direct and indirect impacts of climate change on Congo Basin biodiversity, through field data collection in the Lac Télé Community Reserve, an important conservation area within the Cuvette centrale's Republic of Congo. I gathered observations of change documented by Lac Télé Community Reserve's local population and classified reported adaptation strategies according to potential impacts on biodiversity, following an established framework from the IPBES-IPCC. This chapter is supplemented by an ethnographic study entitled "*Fine-scale human-flood relationships in the Congo Basin: Ethnographic perspectives from the Lac Télé Community Reserve*", which provides an in-depth exploration of local communities' understandings of and adaptations to hydro-climatic dynamics in the Lac Télé Community Reserve (Supplementary material).

Chapter IV: Shrinking climatic space: Implications for forest elephant conservation in the Congo Basin under climate change

In my last chapter, I returned to a regional perspective, focusing on one of the Congo Basin's most ecologically significant species, the African forest elephant (*Loxodonta cyclotis*). Using bioclimatic envelope modeling and an ensemble forecasting approach, I assessed projected shifts in the species' climatic space under climate change, reflecting on difficulties posed by data scarceness, and assessing implications for the long-term conservation of a Congo Basin rainforests keystone species.

Chapter II

Uncertain future for Congo Basin biodiversity: A systematic review of climate change impacts

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Highlights

- Climate change impacts are expected to affect biodiversity in the Congo Basin, the world's second-largest rainforest.
- Our systematic literature review findings highlight an uncertain future trajectory for Congo Basin biodiversity.
- Even if rainforests present adaptive capacities to climate change, deforestation will heighten future ecosystem vulnerability.
- Addressing research gaps on the sensitivity of organisms to climate change, shifts in composition and fruiting changes is crucial.

Abstract

Climate change impacts are expected to affect Congo Basin biodiversity at large scales, with widespread implications in terms of global biodiversity conservation. Through a systematic literature review, we identified 104 peer-reviewed and gray publications highlighting the large variability of observed and projected effects of climate change in the Congo Basin, from genes to ecosystems. Several studies document increased species vulnerability to extinction, shifts in species range and decrease in organism body size. More scattered studies report impacts on species genetics, physiology and phenology. Studies that combine climate change with other drivers of change, such as land-use change or human adaption responses to climate change, cast a bleak perspective for the future persistence of biodiversity in the Congo Basin. Our review highlights the need for investigations on neglected responses, including those related to population dynamics, shifts in plant resource availability and associated ripple effects across ecological levels, as well as the likelihood of large-scale compositional shifts.

Introduction

Climate change impacts biodiversity levels at all levels, from genes to ecosystems. The most documented impacts include distributional shifts, altered phenological patterns, disrupted trophic networks, potential species extinction and ecosystem collapse (Parmesan & Yohe, 2003). In addition to direct impacts, climate change also has indirect impacts on biodiversity, via human adaptation responses that increase the impacts of other threats (e.g., increased habitat loss due to the expansion and displacement of agriculture or increased overexploitation due to higher volumes of illegal wildlife trade, Maxwell et al., 2015). The interaction of climate change with other drivers of biodiversity change, such as land-use change, creates positive feedback loops cascading over ecological systems at multiple spatial and temporal scales (Rockström et al., 2009).

With an extent of 2.87 million km^2 (Malhi & Wright, 2004), the Congo Basin is the second-largest continuous tropical rainforest in the world after the Amazon. Spanning across six countries in Central Africa (Cameroon, the Central African Republic, the Democratic Republic of the Congo, Equatorial Guinea, Gabon and the Republic of Congo), its role in global climate regulation and biodiversity conservation, while sometimes underappreciated, is of global significance (Dezfuli, 2022; Justice et al., 2001). Although above-ground and below-ground carbon stock estimates vary greatly in this area, live biomass carbon stocks show long-term stability in the Congo Basin, in contrast to a declining trend in the Amazon (Hubau et al., 2020). Recently, a mapping exercise of the central Congo Basin depression called Cuvette centrale showed the extent of its peatland complex, the largest in the tropics, storing 29 gigatons of carbon, which is 29% of the planet's tropical peat carbon (Dargie et al., 2017).

Congo Basin rainforests form a composite of diverse forest types, ranging from the Atlantic coastal evergreen forests in Gabon to the semideciduous central part of the Basin (Réjou-Méchain et al., 2021). Ranked third in terms of species richness globally (Mittermeier et al., 2003), these rainforests host remarkable levels of biodiversity (Mallon et al., 2015). Charismatic, critically endangered Congo Basin megafauna includes the African forest elephant (*Loxodonta cyclotis),* bonobo (*Pan paniscus*), western lowland gorilla (*Gorilla gorilla gorilla*) and central chimpanzee (*Pan troglodytes troglodytes*), whose global persistence depends largely or entirely on the conservation of their Congolese populations (IUCN, 2024). The region also provides a livelihood for about 100 million people (Eba'a Atyi et al., 2022), including Indigenous and Local communities relying on forest resources for their subsistence, cultural and spiritual practices (Oslisly et al., 2013). Congo Basin forests are faced by multiple threats, including deforestation and forest degradation driven by agriculture, infrastructure development and extractive industries, as well as illegal wildlife trade and the introduction of invasive species (Tyukavina et al., 2018). Although Congo Basin deforestation rate is low compared to that of other tropical rainforests, it reached 12.46% in the 1990-2020 period and is progressing rapidly (WRI, 2025). Forest intactness decreased from 78% in 2000 to 67% in 2016 (Shapiro et al., 2021). Small-scale agriculture is considered by several authors as a key driver of deforestation (Shapiro et al., 2021; Tyukavina et al., 2018), but large-scale industrial agriculture linked with palm oil, rubber and sugar production also constitutes a major threat (Shapiro et al., 2023). The impact of extractive industries such as intensive logging or mining is magnified by the construction of roads, which improves accessibility and increases human disturbance in remote areas (Kleinschroth & Healey, 2017). In many parts of the Congo Basin, large decline in mammal species leads to local extirpation, with cascading effects across ecosystem levels through disturbance of important processes such as seed dispersal (Abernethy et al., 2016; Beaune et al., 2013). Political instability and armed conflicts are also considered as key drivers of forest disturbance, with effects on hunting, illegal trade and forest resource exploitation (Butsic et al., 2015; Funk et al., 2022). Climate change is expected to amplify those threats.

The understanding of the Congo Basin's complex regional climatic system is limited by the dearth of meteorological data and the absence of long-term, homogeneous climatic records

(Nicholson, 2014). Most climate models project a temperature increase between 1.5 and 6°C by 2100, depending on future trajectories of anthropogenic greenhouse gas emissions and future regional deforestation scenarios (Abernethy et al., 2016; Akkermans et al., 2014; Haensler et al., 2013). However, significant uncertainties remain in terms of regional rainfall projections, with high divergences regarding the direction and magnitude of changes between studies, as well as a discrepancy between observed evidence and projected trends (Asefi-Najafabady & Saatchi, 2013; Maidment et al., 2015). While certain studies showcase a long-term drying trend (i.e., Hua et al., 2016; Malhi & Wright, 2004; Nicholson et al., 2018; Zhou et al., 2014), others conclude from cross-median model analysis that a slight wetting scenario is the most likely (Creese et al., 2019; Ludwig et al., 2013; Wilkie et al., 1999). Available studies at the local level, while rare, tend to corroborate the drying hypothesis (Bessone et al., 2021; Bush, et al., 2020a; Inogwabini et al., 2006, 2011). Uncertainty also exists regarding potential seasonality shifts or the future distribution and frequency of extreme weather events (Abernethy et al., 2016).

Previous literature reviews provide evidence of ongoing reorganization of biodiversity under climate change. In North America, climate change impacts have been reported through behavioral and morphological changes in species, widespread range shifts in taxa and ecosystems, phenological changes linked with migratory patterns and changes in primary production and community interrelationships. Examples include drought-driven physiological stress and large-scale mortality for Sierra Nevada forests in California (Weiskopf et al., 2020). Northward and uphill species shifts are evidenced in Europe (for example, a shift of plants towards higher altitude in the Swiss Alps), and most plant species are projected to shift their distributional range by hundreds of km by the end of the century (Feehan et al., 2009; Milad et al., 2011). Changes in abundance or breeding times were also documented in European bird species (Pautasso, 2012); beetle outbreaks, linked with extreme events, were reported in both North America and Europe (Weiskopf et al., 2020; Milad et al., 2011). Tree line shifts along altitudinal gradients was a common focus of investigation in Central Asia, although geographical barriers in the Himalaya range could prevent large-scale species dispersal (Xu et al., 2009). Although the literature is strongly biased towards the northern hemisphere, impacts are also reported in tropical ecosystems, including increased tree mortality, shifted forest vegetation dynamics and species composition in Southeast Asia, as well as range contraction in China (Deb et al., 2018). In the Amazon, future climate projections report considerable ecosystem shifts, including forest loss and forest succession, from evergreen forest to mixed forests or grassland, as well as savanna extension (Marengo et al., 2011). One study highlights increased range reduction and local extinction risks for species in Africa (for example the ecological specialist *Canis simensis*) in response to a declining access to natural resources (Sintayehu, 2018). The Congo Basin was however excluded from that review.

This study aims to identify and characterize the current state of knowledge addressing climate change impacts on Congo Basin biodiversity, at all of its organizational levels. Following a systematic review methodology, we delineate current knowledge clusters and research gaps. In particular, we discuss findings from the literature based on the following questions: how does biodiversity respond to climate change in the Congo Basin? What are the literature foci in terms of biodiversity organizational levels and core ecological processes? Which type of responses are already observed, and which ones are projected in the future?

Methods

We systematically examined scientific literature linked with current and projected climate change impacts on biodiversity in the Congo Basin. The review followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) framework (Page et al., 2021). We started the review process in February 2022 with a literature-scoping process in which the review strategy, objectives and search questions were identified. We defined search keywords (Table 1) a priori and then refined them through an iterative process that comprised several search cycles. We adapted keywords related to biodiversity variables from Pacifici et al. (2017). We constructed query strings using the selected keywords as well as the Boolean operators AND and AND/OR. We applied the same process to the definition of inclusion/exclusion criteria, as well as search filters, which were refined once a finer knowledge of the literature was gained. The first author performed the final search in November-December 2022 and updated it in May 2024, using the SCOPUS and Web of Science platforms, with specific filters used through advanced search criteria (see Supplementary material for the full list of performed queries and filters). We integrated articles identified through citation tracking in the final list, to obtain a comprehensive literature sample. In order to mitigate potential knowledge gaps in the published literature, we extended the search to gray literature studies, identified using the Google Search Engine, and by consulting the repositories of specialized organizations operating in Central Africa, including the Center for International Forestry Research (CIFOR), the Stockholm Environment Institute and the Central African Forests Commission (COMIFAC). After an initial review of the available literature, we opted to use

English keywords only for the search in the bibliographic databases, given the absence of relevant studies meeting our selection criteria in French. However, we also conducted gray literature searches in French, considering its widespread use in the studied region. To understand the relative size of the literature on climate change impacts on biodiversity in the Congo Basin, we completed similar literature searches targeting the Amazon region (Supplementary material).

Table 1: Keywords and search variables.

Search terms	
Location	Congo Basin, Central Africa, tropical Africa, Equatorial Africa, African rainforest, Central African rainforest, tropical African rainforest, Afrotropical region, Cameroon, Central African Republic, Democratic Republic of the Congo, Democratic Republic of Congo, DRC, DR Congo, Congo, Republic of the Congo, Republic of Congo, Gabon, Equatorial Guinea
Variable 1	Global warming, climate change, drought, flood, CO_2 concentration, El Niño event, La Niña event, forest fire, extreme weather event, seasonality, sea-level rise, precipitation, heat
Variable 2	Biodiversity, rainforest, wildlife, species, mammals, carnivores, herbivores, ungulates, primates, rodents, reptile, birds, fish, insects, population reduction, population decline, increase in population size, range changes, range shift, range reduction, turnover, extinction risk, extinction probability, survival, mortality, fertility, reproduction, changes in phenology, advances in migration, adaptation

We assessed collected publications for eligibility through a three-step screening process, by: 1) screening the title, 2) screening the title and the abstract and 3) reading the full text. A publication was considered eligible for inclusion if it explicitly considered the targeted geographic unit and the inclusion variables (Table 1). For this study, we considered exclusively publications related to the ecoregions listed by Olson et al. (2001) in the Congo Basin area (Figure 1). Studies located outside Congo Basin ecoregions, including those pertaining to countries such as Angola or Zambia, which are part of the hydrographic definition of the Congo River Basin, were excluded from the review. We also excluded palaeoecological studies referring solely to past climate change and studies focusing exclusively on climate change impacts on Congo Basin carbon stocks or hydrology, without an explicit link with biodiversity. We analyzed literature review findings through a thematic and narrative synthesis method and classified results, following an approach adapted from the frameworks established by Bellard et al. (2012) and Scheffers et al. (2016, Supplementary material).

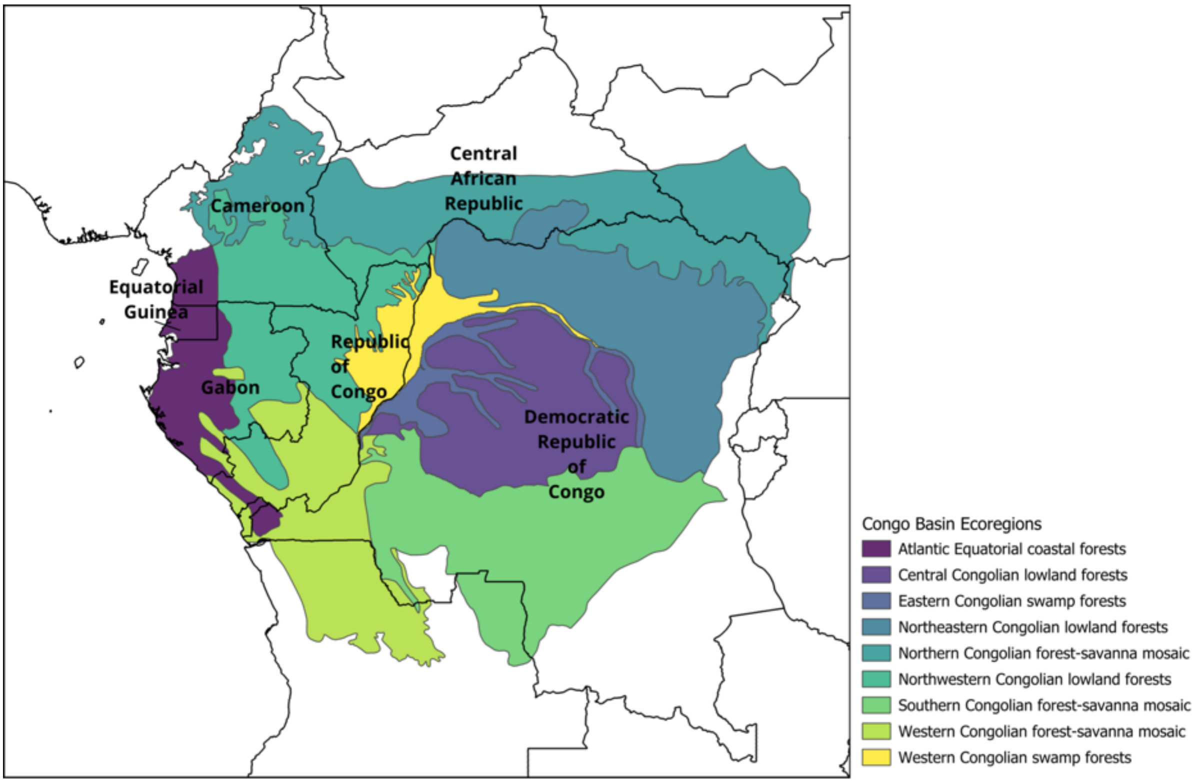

Figure 1: Map of Congo Basin ecoregions (according to Olson et al., 2001).

Results

The literature search on climate change impacts on biodiversity in the Congo Basin returned 2,000 papers. In comparison, the search on the Amazon rainforest returned approximately five times more results (10,611). After the screening process, we retained a total of 104 publications, including 12 gray publications, published between 1996 and 2024, and describing 105 impacted ecological processes. Of the reviewed publications, 29% focused on the response of tropical forest ecosystems to climate change, while 22% examined mammal species responses. Another 19% and 11% of studies discussed climate change effects on plant and bird species respectively, while less than 8% focused on other taxonomic groups, such as insects, reptiles and amphibians.

The future distribution of invasive species in the Congo Basin was the focus of 11% of publications, specifically regarding plant and insect species.

Shift in species distributional range was one of the most studied ecological process responses (20%), followed by studies examining the potential of ecosystem state shift (17%) or impacts on species physiology (14%, Figure 2). In contrast, few studies focused on climate change impacts on ecological processes at lower organizational levels. Species genetics or morphology have been explored only in a few studies (6 and 7%, respectively). Climate-change driven phenological shifts were investigated in 3% of the studies. It is noteworthy that retrieved studies consisted of a majority of ecological modeling studies (58%), rather than responses observed *in situ* (32%), followed by synthesis reports (10%). Field observations represent 13% of studied responses, followed by remote sensing imagery (9%), ecological observations from local communities (7%) and experiments (3%).

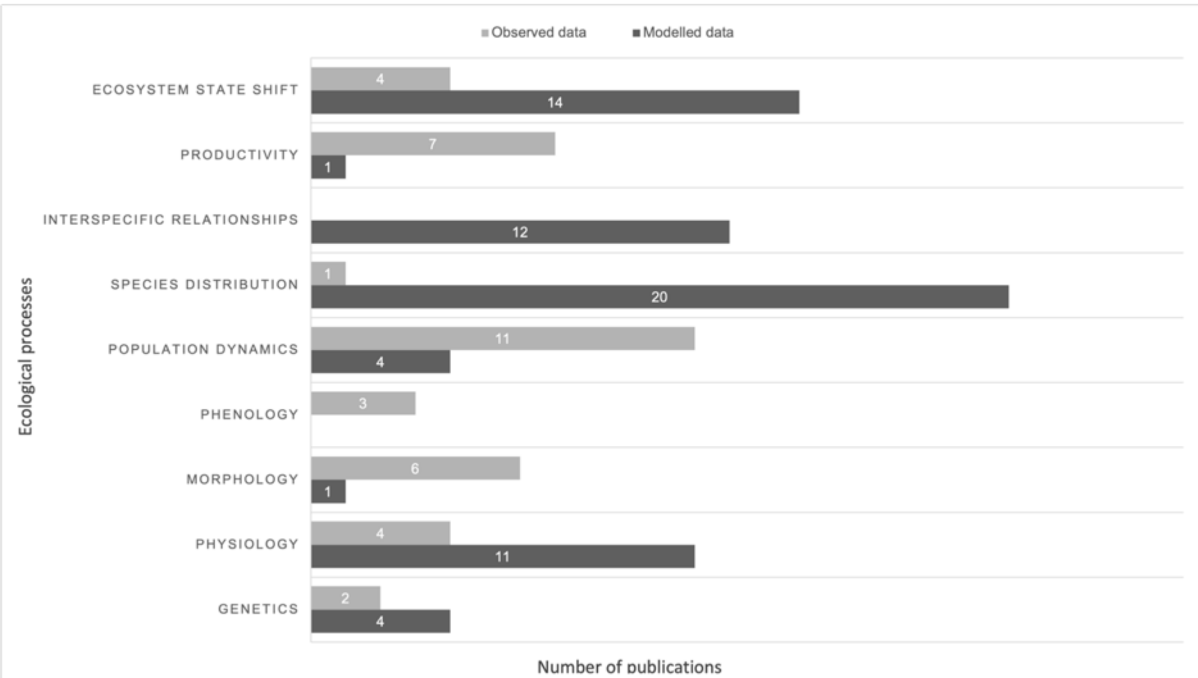

Figure 2: Literature distribution in terms of studied ecological processes (n=105 impacted processes).

Genetics

We found six studies assessing the evolutionary potential of species in the face of climate change, with a focus on *Bicyclus dorothea* (a Central African butterfly), the puddle frog (*Phrynobatrachus auritus*), the little greenbul bird (*Andropadus virens*), the rodent Misonne's praomys (*Praomys misonnei*) and the Lepidosauria clades. Dongmo et al. (2021a) demonstrate that *Bicyclus dorothea* exhibits greater thermal tolerance when originating from ecotone habitats (transitional zones between forest and savanna ecosystems) compared to those originating from closed canopy rainforests with stable temperatures. Zhen et al. (2023) confirm the greater phenotypic plasticity of the ecotone populations of *Bicyclus dorothea*. High levels of genomic vulnerability were found in southwestern Gabon, in the Cameroonian Sanaga River delta area and north of the Lobéké and Nki National Parks for *Phrynobatrachus auratus* and *Praomys misonnei* (Miller et al., 2020; Morgan et al., 2020). Diele-Viegas et al. (2020), evaluating climate change impacts on the phylogenetic patterns of Lepidosauria, a clade including lizards, snakes and amphisbaenians, suggest a higher ratio of species negatively affected in the Afrotropical realm compared to other regions. Under a RCP 4.5 climate change scenario (Representative Concentration Pathways scenarios are described in the Supplementary material), the little greenbul would necessitate a substantial genomic shift potentially exceeding biological limits, especially when also considering socio-economic threats such as mining and large-scale agriculture. Interestingly, the amount of genomic shifts required to match environmental conditions will also be lower for greenbuls occurring in an ecotone habitat.

Physiology and morphology

Few observational evidence of climate change effects on species survival was found in the literature. In the Cameroonian Campo Ma'an, Mbam Djerem and Lobéké National Parks, described as amphibian diversity hotspots, an increased annual precipitation is projected to favor the spread of the infectious disease Chytridiomycosis, a chief factor of amphibian decline (Miller et al., 2018). The pallid swift (*Apus pallidus)*, a migratory bird wintering in West and Central Africa, displays reduced survival in its wintering area when confronted with extreme droughts or rainfall events (Boano et al., 2020).

A pantropical modeling exercise finds that the effects of the El Niño–Southern Oscillation (ENSO) events of 1997-1998 and 2015-2016 on Equatorial African tree growth were low to moderate, compared to the Amazon or Southeast Asian rainforests (Rifai et al., 2018). However, climate change impacts on tree growth and wood formation are observed *in situ*. In the Central African Republic, increasing drought leads to reduced growth in semi-deciduous tree species (Ouédraogo et al., 2013). Among the studied group, slow-growing, shade-tolerant evergreen species, considered more conservative in their resource use, are less sensitive to climatic changes, which could favor a compositional shift towards such species in the future. In a study comparing tree growth in three Democratic Republic of the Congo locations, evergreen species, showing large anatomical variability in sites where the precipitation seasonality was the most marked, conversely appear to be more sensitive to precipitation changes than their deciduous counterparts (Tarelkin et al., 2019). With increased temperature, tree growth is shown to be significantly decelerating in three light-demanding species (*Entandrophragma cylindricum*, *Triplochiton scleroxylon* and *Erythrophloeum ivorense*) near the Lobéké National Park, despite increasing CO_2 atmospheric concentration (Battipaglia et al., 2015). Increased aridity is also found to affect the growth, also impacting fruit production and dispersal ability, of *Sarcophrynium prionogonium* (Ley et al., 2018), a widespread perennial forest understory species from the Marantaceae family, considered a staple food for western lowland gorilla (Magliocca & Gautier-Hion, 2002). In Hatangi et al. (2023), five understory shrub species (*Coffea canephora*, *Hua gabonii*, *Scaphopodous thonneri*, *Tabernaemontana penduliflora*, *Uvariopsis solheidii*) conversely seem to have developed larger leaves in response to increasing temperature.

For insects, observations from local communities in the Central African Republic suggest that caterpillar species such as *Imbrasia oyemersis*, *Pseudantheraea discrepans* or *Imbrasia trunctata* are now smaller and have a shorter lifespan, which affects the quantity of caterpillars consumed by households (a decrease in weight of 86%, Sonwa et al., 2020). In the Gabonese Lopé National Park, a photographic database documented an 11% decline in the body mass of the forest elephant from 2008 to 2018 (Bush, et al., 2020b). This phenomenon correlates with a precipitation decline and a significant decrease in fruiting events. Although forest elephants have a versatile diet, increased fruit scarcity could result in additional impacts, such as reduced fitness or increased disease risk, and affect their ability to cope with other environmental stressors.

Phenology

While phenological shifts have not been explored in ecological modeling, we found documentation of such observations in a few species, including plants, insects and birds. In Gabon (see the "Physiology and morphology" section), an 80% decrease in fruit production in 73 tree species reported over a 32-year period in the Lopé National Park is described as a "*fruit collapse*" (Bush et al., 2020b). Fruits are an important resource for many nectarivorous or frugivorous taxa and impacts linked with disturbance of plant reproductive phenology could occur without being recorded across other taxonomic groups. Tutin et al. (1997), cited by Korstjens & Hillyer (2016) observe that fruit scarcity would lead to a diet shift in two Lopé primate species during the dry season, but that chimpanzees, as well as guenon species such as *Cercopithecus nictitans*, would not exhibit such dietary flexibility, which could increase their vulnerability to droughts. Bush et al. (2020b) propose that rising temperatures may compromise the reproduction of many Congo Basin trees, as their reproductive cues linked to a temperature decline during the dry season could vanish. However, considering the variation in leaf shedding, flowering or fruiting phenological patterns, factors such as rainfall fluctuations, evapotranspiration or solar irradiance could also play crucial roles in regulating these cues for tree species (Ouédraogo et al., 2020). Unfortunately, long-term phenology records are lacking, hindering our understanding of how climate change, including extreme events, will impact these processes (Butt et al., 2015; Chapman et al., 2005; Couralet et al., 2010).

In the Central African Republic, local communities observe that an early rainy season leads to the earlier appearance of *Imbrasia oyemersis*, *Pseudantheraea discrepans* or *Imbrasia trunctata* caterpillars (in May rather than June, Sonwa et al., 2020). An advance in the start of the main migration period and a slight delay in the end of the wintering time are also observed in several tropical African bird species, thus resulting in a widening of their migration period (Maggini et al., 2020). Implications of shifting migration in terms of predator-prey asynchronicity are discussed in Coppack et al. (2008): a shift in spring phenology affects the insectivorous Pied flycatcher's (*Ficedula hypoleuca*) ability to feed on invertebrates when arriving in its breeding grounds. Due to a lack of photoperiodic incentive, the Pied flycatcher might be unable to adjust its departure from its wintering grounds in West and Central Africa.

Population dynamics

We found both observational and predictive data linked to abundance reduction driven by climate change in the Congo Basin. In the Central African Republic, local communities observed an 88% drop in edible mushrooms (Sonwa et al., 2020). A similar decline in mushrooms, honey, crabs and caterpillars is reported near the Democratic Republic of the Congo Kahuzi-Biega National Park (Batumike et al., 2021). Afro-Palaearctic migrant birds wintering in tropical Africa, such as the tree pipits (*Anthus trivialis*), the European turtle doves (*Streptopelia turtur*), the common cuckoos (*Cuculus canorus*) and the spotted flycatchers (*Muscicapa striata*), are shown to experience a more rapid decline than species migrating to other African regions, with suggested links to regional changes in climate and land-cover (Tutin et al., 1997).

A 3 to 8% decrease in the abundance of the 76 most common Gabonese forest species is projected by the end of the century, with species-specific differences in the direction of change (one-third of the sample species is projected to increase in abundance and another two-third is considered likely to decline, Núñez et al., 2022). An analysis of 12 tree and palm species within the central Congo Basin also anticipates cross-taxa differential responses, with three deciduous species (*Ceiba pentandra*, *Lophira alata* and *Pericopsis elata*) projected to face the most substantial biomass loss (Dury et al., 2018). Based on data obtained from 105 logging concession inventories, Réjou-Méchain et al. (2021) establish that, in 10 forest types, current climatic niches will vanish or shift at spatial and temporal scales surpassing tree dispersal ability. Ting et al. (2012) hypothesize that current and future climate change trends could lead to a 15-fold population decline of the drill (*Mandrillus leucophaeus*) in the future.

Distribution

Distribution shifts or range loss in Congo Basin species have not been observed *in situ*, but they are projected across several taxonomic groups. McClean et al. (2005) show a progressive loss of areas of suitable climate for plant species in the Guineo-Congolian rainforests, including the central Congo Basin. Reduced distributional range is projected in several endemic species, including the legume species *Angylocalyx oligophyllus* (Oyebanji et al., 2021), the genus *Talbotiella* (Asase et al., 2021) and the rainforest understory shrubs *Dracaena camerooniana* (Bogawski et al., 2019). In Gabon, 21 keystone African palm rainforest species are projected to experience a loss of climate suitability in about 70% of their range and would have to disperse by more than 100 km to keep track of their preferred climatic conditions (Blach-Overgaard et al., 2015). In contrast, range expansion is expected to occur in four water lily species by 2050 (*Nymphaea nouchali*, *N. micrantha*, *N. lotus* and *N. heudelotii*) (Nzei et al., 2021). A sample of 40 socio-economic important NTFP species (e.g. *Senegalia senegal* or *Garcinia kola*) are projected to experience distributional range gain under a RCP 4.5 scenario, but most would lose climate suitability under RCP 8.5 trends (Amoussou et al., 2022).

Rare studies considering insects project increased future climate availability in Central Africa for the flies *Sarcophaga dux* and *Sarcophaga haemorrhoidalis* and the dragonfly *Pantala flavescens* (Al-Khalaf et al., 2023; Liao et al., 2023). Jetz et al. (2007), considering the interactions between climate and land-use change, project large range contractions for Congo Basin bird species by 2100, mainly reflecting large-scale agricultural conversion (Jetz et al., 2007). In contrast, Hole et al. (2011) demonstrate that all Congo Basin Important Bird and Biodiversity Areas (IBAs) will conserve climate suitability for bird species, attracting significant numbers of colonists from other regions. Modeling evidence indicates a northward range shift of about 3.45 km per year for the barn swallow (*Hirundo rustica*) population wintering over West and Central Africa throughout the 20th century. The increasingly warmer and drier ecological conditions in its new wintering areas may diminish the population's carrying capacity (Ambrosini et al., 2011). Species with limited dispersal abilities, such as the endangered Congo peafowl (*Afropavo congensis*), may face additional challenges through the flat topography of the Congo Basin, necessitating migration over larger large distances to track its climatic niche (Şekercioĝlu et al., 2012).

Among African regions, the Congo Basin is forecasted to experience the highest rate of mammal species loss due to future climate and land-cover changes (a 50 to 60% loss in 2050, depending on climate scenarios and assuming no dispersal, Thuiller et al., 2006). Carvalho et al. (2021) estimate that climate and land-use change will accelerate loss for most great apes, including Grauer's gorillas (*Gorilla beringei graueri)* and central or eastern chimpanzees (*Pan troglodyte troglodytes* and *Pan troglodytes schweinfurthii*), which are expected to lose most of their range in all future scenarios. In a worst-case scenario, the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*) will also see a quasi-disappearance of climatically suitable habitat in the Congo Basin (Sesink Clee et al., 2015). However, Carvalho et al. (2021) note that habitat gain could also occur if species are able to disperse. The *Colobus* genera will see a marked decrease of climatically suitable areas, whereas projections are more contrasted for *Cercopithecus* species, which will also see new habitats becoming available (Korstjens, 2019). The African wild dog (*Lycaon pictus*) is projected to lose a significant part of its Congo Basin habitat, likely due to the future presence of the African lion (*Panthera leo*) as a main constraint for its occurrence (Jones et al., 2016). The sole study examining on climate change impacts on African pangolins reveals varying effects on habitat distribution across taxa (Dury et al., 2018; Xian et al., 2022). Fragmented habitats for the giant pangolin (*Smutsia gigantea*) could connect into larger areas, leading to a significant habitat increase (a growth rate of 211% under the SSP 585 scenario). Conversely, the long-tailed pangolin (*Phataginus tetradactyla*) is anticipated to undergo a substantial shift towards the central and western Congo Basin, with its eastern habitat completely disappearing. Meanwhile, the tree pangolin (*Phataginus tricuspis*) is projected to migrate from the north to the southern Congo Basin.

Interspecific relationships

We found evidence that distributional changes induced by climate change promote novel interspecific interactions in the Congo Basin. In the M'Baïki region, located in the Central African Republic, climate change accelerates tree growth, mortality and recruitment, with differentiated impacts across species, which is expected to cause changes in flora assemblage, favoring long-lived pioneers at the expense of shade-bearer species (Claeys et al., 2019). Potential community disruption could also occur through the spread of invasive alien species.

Under an RCP 8.5 scenario, an increase in the range of the lantana (*Lantana camara*), one of the most invasive alien plant species worldwide, is projected in several African countries, especially in northwestern Congo and eastern Gabon (Qin et al., 2016). Goncalves et al. (2014) also project areas of vulnerability for lantana invasion in the Democratic Republic of Congo, Cameroon and Central African Republic. Future climatically suitable areas for the field sandbur (*Cenchrus spinifex)*, an annual grass renowned for its negative impacts on species diversity and community productivity, include Central Africa, with pockets of medium risk in the northern Congo (Cao et al., 2021). For the Chilean needle grass (*Nassella neesiana)*, areas of high future climate susceptibility will include the eastern Democratic Republic of Congo and northern Gabon (Bourdôt et al., 2012). A study focusing on the top 100 invasive species, such as the Asian tiger mosquito (*Aedes albopictus*) or the brown catsnake (*Boiga irregularis*), finds that, even though environmental suitability for invasive species will decrease in the future, the Congo Basin could still maintain favorable climatic conditions for a large pool of species (i.e., 20 to 40 new invasions, Bellard et al., 2013). Medium invasion risk suitability is projected for the yellow crazy ant (*Anoplolepis gracilipes,* also listed among the top 100 invasive alien species) in most of the Congo Basin, with areas of higher risk in the central Democratic Republic of the Congo and at the border with the Republic of Congo (Chen, 2008). The Argentinian ant (*Linepithema humile*) is expected to gain climate suitability in the entire Central Africa, except in the central Democratic Republic of the Congo, where models project high rainfall (Jung et al., 2022). Both species are the cause of ecological concerns, being known for preying upon hatchling birds, reptiles and small mammals, or affecting native arthropod populations. On the contrary, an invasive fly species (*Drosophila nasuta*) currently observed in the western Congo Basin will see a range contraction in the northwestern Democratic Republic of the Congo under a SSP 245 scenario, and additionally in the northeastern and southern Democratic Republic of the Congo under SSP 585 (Lauer Garcia et al., 2022).

Ecosystem productivity

There is mixed observational evidence with regard to the effects of climate change on Congo Basin rainforest biomass production and matter flux. Through satellite-borne remote sensing data, Zhou et al. (2014) detect water content changes and a gradual vegetation browning, especially in the northern Congo Basin, which could result from a long-term drying of the upper forest structure, leading to decreased photosynthetic capacity. This result is questioned by Sun et al. (2022), who do not detect any signal of long-term droughts on forest productivity, looking at long-term MODIS datasets. Moparthy et al. (2019), highlighting the inherent uncertainties linked with remote sensing data, note that failing to consider the upward aerosol trend occurring over the Congo Basin could lead to an artificial browning signal of up to 8%. Bennett et al. (2021) consider the impacts of the 2015-2016 ENSO record drought, which came in addition to a documented 50-year decreasing rainfall trend, on 100 inventory plots located across several Congo Basin countries. Similar to Rifai et al. (2018), the authors conclude that no significant effect on carbon mass dynamics is observable. Similarly, a remote sensing-based vegetation index records an increase in net primary production trends in Central Africa from 1982 to 2011, in spite of increasing temperatures (Gao et al., 2016). In response to increasing CO_2 concentration, Central African plants are projected to reduce future water stress, primarily through enhanced evapotranspiration (Swann et al., 2016). However, Bauters et al. (2020) observe a decreasing water use efficiency in Congo Basin tree species, a response contrasting with the expected impacts of increasing CO_2 on plants, which could be explained by the mediating role played by warming temperature.

Ecosystem state shift

Findings from both modeling and observational studies present a mixed picture. On one hand, it is considered likely that, considering their colder and drier climate, Congo Basin forests will exhibit greater resistance to climate change impacts, compared to their American or Southeast Asian counterparts. Congo Basin tree species could be more resilient to droughts, due to an evolutionary history of large-scale climatic and ecological shifts (Abernethy et al., 2016). It is speculated that the occurrence of megafauna species could also contribute to Congo Basin rainforest resilience: the role of forest elephants in tree seed dispersal and tree felling is an often-cited example of megafaunal contribution to ecosystem resistance against state shifts (Malhi et al., 2016). This view is corroborated by studies such as Núñez et al. (2022, see "Population dynamics" section) which show that climate change-driven tree species loss could be more contained in the Congo Basin compared to other parts of the world, such as in the Neotropics, where a 30 to 50% loss in species richness is projected. Zelazowski et al. (2011) project increasing precipitation trends in a +4°C scenario, triggering a forest expansion in the Congo Basin margins, while Yu et al. (2014), who also anticipate an increase in precipitation along with CO_2 enrichment, project an expansion of deciduous tree species at the expense of C4 perennial grass, and an increase in evergreen tree abundance. Despite experiencing severe droughts in 2005 and 2010, Central African forest did not exhibit structural canopy alteration in remote sensing imagery, which can be interpreted as a sign of ecosystem resilience to water stress impacts (Asefi-Najafabady & Saatchi, 2013).

Climatic conditions within the Congo Basin may also render its forests less tolerant to increasing temperatures, particularly if they are already nearing their thermal optimal. Tang (2019) hypothesizes that, in the eventuality of a rainfall collapse, Congo Basin rainforests could experience regional-scale shifts to savanna ecosystems. When considering both future climate and land-cover changes, a 27% tree cover loss is projected in Cameroon, the Central African Republic, Equatorial Guinea and Gabon, with additional forest fragmentation in the Democratic Republic of Congo and the northern Republic of the Congo, even under a RCP 2.6 scenario (Aleman et al., 2016). In contrast, Singh et al. (2022) evidenced a decline in the ability of forest ecosystems to sustain stable conditions, attributed to escalating climate risks and feedback interactions with regional anthropogenic land-use change. Their findings suggest that the most stable forest ecosystems are situated in the central Congo Basin, and that the least stable forests are found in the northern and southern parts of the Congo Basin rainforests, considering both projected precipitation trends and root zone storage as an indicator for drought buffering capacity.

Species vulnerability to climate change

The Congo Basin is recognized for its high rate of primate vulnerability to climate change impacts, considering factors such as its species richness, their current endangered status and projected climate change trends (Graham et al., 2016). In West and Central Africa, 16% and 8% of 150 primate taxa are considered to be moderately to highly vulnerable to drought (Zhang et al., 2019). Despite its low projected exposure to future climate change, the Congo Basin is also listed among the regions with the highest proportion of vulnerable birds, due to a high concentration of species with low adaptive capacity and high sensitivity to climate change impacts (Foden et al., 2013). In a more recent study (Buchan et al., 2022), bird species migrating to Central Africa during winter are conversely considered to be less vulnerable in terms of exposure to threats and susceptibility to direct mortality risks than species wintering in Eastern and Southern Africa, where the frequency of extreme climatic events is considered higher. Contrary to Foden et al. (2013), a study focusing on 195 species of Sub-Saharan African amphibians projects high future vulnerability in the Congo Basin, with a high proportion of species losing future local suitability and a high overlap of climate risk exposure and low temperature tolerance (Garcia et al., 2014).

Interactions with other threats to biodiversity

Even if Congo Basin rainforests present adaptive capacities to increasing temperature and varying duration of droughts, future deforestation and forest fragmentation for agriculture, infrastructure development or extractive activities will significantly increase future ecosystem vulnerability (Tang, 2019). Although insufficiently assessed, the interactions between climate change and anthropogenic land-cover change will significantly reduce rainforest resilience and accelerate species habitat contraction even further. In all studies considered in our review, land-use change was, almost systematically, identified as a primary driver of change, regardless of the severity of projected climate change (Aleman et al., 2016). A combination of impacts from climate change and logging concessions is suggested to negatively affect 35 to 74% of Congo Basin biodiversity, with logging concessions occurring in projected low climate risk areas (Asner et al., 2010). Such approaches have been adopted in a minority of studies identified through this review, but should be widely replicated, considering risks in terms of biodiversity loss.

Additional global change drivers, such as the overexploitation of natural resources, are expected to instigate reinforcing feedback loops with the impacts of climate change in the Congo Basin. In this context, indirect impacts of climate change on Congo Basin biodiversity processes, brought about by local human communities' responses to changing environmental conditions, are rarely considered, even though induced changes on forest dynamics could be profound (Leblois, 2021). Such instances of have been evidenced in a few sites: in the Sangha Tri-National landscape (Chia et al., 2016) and the Democratic Republic of the Congo Ituri Forest (Wilkie et al., 1999), local communities been shown to compensate for climate change-driven decline in agricultural yields by expanding crop production into forested areas. Local communities may also turn to increased involvement in hunting or fishing activities to compensate for climate-change induced livelihood loss. Advancing our comprehension of local communities' adaptive strategies and resultant biodiversity impacts should be considered as an urgent line of future research.

Discussion

As substantiated through the observational evidence and predictive data found in the literature, a variety of biodiversity responses to climatic changes is already apparent in the Congo Basin, across all biodiversity organizational levels. Among the most studied responses, climate change in the Congo Basin is projected to increase species vulnerability across taxonomic groups, including primates and birds, and to restrict the distribution of several species, especially large-bodied mammals such as great apes, affecting population abundance. Certain organisms, including the forest elephant, are reducing in size in response to increased temperature and changed rainfall conditions. Projected future climatic conditions are expected to be conducive to biological invasions. All in all, it is expected that the large variability between Congo Basin sites will result in diverse impacts across different forest types.

However, an alarming level of research gaps still remains, which render assessments of ongoing changes and future projections difficult. Many potential impacts on Congo Basin ecological processes are undocumented. For example, climate change-driven evolutionary adaptation, or impacts on trophic level connections and species thermoregulation, hybridization or reproductive rates (with some exceptions: see Dongmo et al., 2021a, or Nanga Nanga et al., 2021) are virtually unknown. Entire taxonomic groups, including freshwater organisms, amphibians, or reptiles are almost completely excluded from the analyzed literature, which is more likely to reflect a research deficit than an absence of impacts (Scheffers et al., 2016). For example, while it is known that 41% of African fish species possess traits characterizing them as highly vulnerable to future climate change, even under a semi-optimistic RCP 4.5 scenario (Nyboer et al., 2019), no similar study exists for freshwater species in the Congo Basin. Moreover, most studies struggle with accounting for biotic interactions (with the notable exception of Jones et al., 2016, on *Lycaon pictus*) and for future species dispersal, which will be key factors in future community response. Sometimes, results appear contradictory (see Ouédraogo et al., 2013, and Aguirre-Gutiérrez et al., 2019 who report opposing directions of change linked with the relative sensitivity of evergreen and semi-deciduous tree species to droughts and compositional changes).

The heterogeneity of results also reflects the diversity of methods employed to assess current and future responses, ranging from remote sensing, ecological modeling, field observations, experimental setups and local ecological knowledge, among others. While this diversity of approaches has benefits, each of them present theoretical or methodological limitations. Satellite imagery products may provide valuable information at large geographical scales, but they are associated with inherent uncertainties, including differences in data acquisition between satellites with polar or geostationary orbits. In ecological bioclimatic envelope or dynamic vegetation models, projected biodiversity responses vary significantly according to the model structure, underlying model assumptions, chosen climatic scenario and baseline climate data (Baker et al., 2016). Because of insufficient local field monitoring and long-term datasets, few studies provide empirical evidence of climate change-driven ecological response, which leads to difficulty in ground-truthing modeling or remote sensing outputs.

In 2021, Congo Basin environmental ministers emphasized the risks associated with insufficient research in the region and called for a substantial investment program (White et al., 2021). Indeed, data gaps identified through our study are indicative of the under-researched status of Congo Basin rainforests, despite their known diversity and species richness, compared to other globally significant tropical rainforests. With ongoing deforestation, land degradation and increasing drought frequency, Amazon rainforests are faced with risks of large-scale dieback (Boulton et al., 2022), carbon storage capacity loss (Brienen et al., 2015) and long-term erosion in species richness (Moulatlet et al., 2021; Stouffer et al., 2021). In this context, the profound global importance of the Congo Basin rainforests is unequivocal. Nevertheless, our study highlights substantial uncertainties surrounding the future persistence of Congo Basin biodiversity in the face of current and future global changes. Therefore, we consider it imperative to allocate additional research resources to address the gaps identified through our literature review, including pressing research inquiries: how sensitive are Congo Basin organisms to warming temperature, considering their limited exposure to interannual thermal variability? What is the extent of flowering and fruiting phenology changes among Congo Basin trees, and with what implications across taxonomic groups? Are compositional shifts already occurring, similar to that documented in a Ghanian forests in response to reduced rainfall (Fauset et al., 2012)? Could warmer temperatures induce peat decomposition, endangering important ecosystems in the Cuvette centrale swamp forests (see Garcin et al., 2022)? Lastly, what defines tipping points within Congo Basin ecosystems? The preservation of the ecological integrity of Congo Basin ecosystems holds ramifications of planetary scale. It is urgent to start paying closer attention now.

Chapter III

"We saw fish in the cocoa farm": Local observations of the impacts of climate change on biodiversity and livelihoods in the Lac Télé Community Reserve, Congo Basin

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Abstract

In the second-largest continuous tropical rainforest in the world, the Congo Basin, climate change affects biodiversity as well as forest-dependent local communities. In the region, the lack of historical biophysical data prevents a comprehensive analysis of climate change impacts on its biophysical systems. In this context, local ecological knowledge, building on local communities' long history of interactions with their environment, can improve the understanding of interwoven environmental changes linked with climate change and biodiversity loss. This study, focused on four villages ranging from seasonally flooded to *terra firma* forests, involved 80 semi-structured interviews, 111 structured interviews and 8 focus groups to document local climatic changes, biophysical impacts and perceived drivers of change through the knowledge of local communities. We also classified adaptation responses into different categories according to their potential impacts on biodiversity. Results suggest that a wide range of climate change impacts is already apparent in the area, including changes in temperature and precipitation and the magnitude of flooding events. Associated impacts on local biodiversity have also been observed, ranging from increased tree mortality, disrupted fish reproduction, disrupted migratory patterns in mammal species and reduced fruit production. Our study filled an important knowledge gap, investigating both the direct impacts of climate change on biophysical systems, and its indirect impacts. Our results highlight the importance of integrating local ecological knowledge in rapid biodiversity change assessments.

Introduction

Along with other drivers of change such as land-use change and the overexploitation of natural resources, climate change increasingly appears as a primary threat to biodiversity conservation (IPBES, 2019) with effects on all biodiversity organizational levels, from genes to ecosystems, and across most ecological processes essential to ecosystem functioning (Bellard et al., 2012, Scheffers et al., 2016). Changes in human behavior in response to climate change, referred to as indirect impacts of climate change on biodiversity, can also create new risks for biodiversity conservation (Segan et al., 2015). As the world's second-largest continuous track of tropical rainforest, the Congo Basin plays a crucial role in global climate mitigation and acts as a key center of global biodiversity, hosting 282 threatened species (IUCN, 2024). Spanning across six countries (Cameroon, Central African Republic, Democratic Republic of the Congo (DRC), Equatorial Guinea, Gabon and Republic of Congo), the rainforests of the Congo Basin support approximately 100 million people from Indigenous Peoples and Local Communities (IP&LC) who rely on forest resources for their livelihoods, cultural and spiritual traditions (Eba'a Atyi et al., 2022). Those rainforests are however faced with multiple threats, including illegal wildlife trade, deforestation and forest degradation driven by small-scale and industrial agriculture, extractive industries, infrastructure development and road construction (Shapiro et al., 2021), which are expected to be further exacerbated by climate change. Despite their global significance, the Congo Basin suffer from a research deficit, driven by the absence of long-term records and the many temporal and spatial gaps in instrumental measurements (Beekmann et al., 2024). Data unavailability impedes the quantification of global and climate change impacts, the identification of emerging trends linked with ecosystem dynamics and the prediction of future patterns associated with climate change and biodiversity loss. Consequently, there is a lack of consensus over future regional rainfall trends, a critical determinant of future ecosystem dynamics: some studies indicate a long-term drying trend (Zhou et al., 2014), whereas others project a slight increase in precipitation (Creese et al., 2019). Local ecological knowledge, defined by IPBES, as "*knowledge about nature, including organisms (animals and plants), ecosystems, and ecological interactions, held by local people who interact with and use natural resources*" (IPBES, 2025), can be crucial in detecting overlooked trends linked to climate and biodiversity. Due to their historical relationships with plant and animal species, as well as abiotic factors within their landscapes, IP&LC are well placed to detect changes in ecological processes within the biophysical systems that underpin their livelihoods (Schulz et al. 2019). Local ecological knowledge is particularly valuable in remote and data-deficient sites (Reyes-García et al., 2024a), and can provide critical insights into the interconnections between ecosystem changes, elucidating the underlying drivers and highlighting the effects on IP&LC livelihoods and socio-cultural conditions (Berkes et al., 2000). In Africa, few studies have relied on information derived from local ecological knowledge to monitor ecosystem dynamics. Nyadzi et al. (2021) provides a review of the role of indigenous knowledge in characterizing and adapting to climate change in Africa. Ayanlade et al. (2017) and Nyadzi et al. (2020) both found associations between indigenous observations and local meteorological stations. In Kenya, Cuni-Sanchez et al. (2019) highlighted the usefulness of local ecological knowledge to fill research gaps in African mountainous areas, and Cuni-Sanchez et al. (2022) documented adaptation strategies used in smallholder coffee farming system. Batumike et al. (2021) investigated local communities' perceptions of climate changes and adaptation strategies in the Albertine Rift. In the Congo Basin, local ecological knowledge of current climatic and ecological changes remains insufficiently documented.

In this context, this study aims to characterize the direct and indirect impacts of climate change on biodiversity on a Congo Basin site, the Lac Télé Community Reserve, Republic of Congo, through the observations of local communities. Part of the largest transboundary Ramsar site in the world (shared with the DRC), the Lac Télé Community Reserve hosts a rich biodiversity and is home to 48 ethnic groups (Devers et al., 2006; Poulsen & Clark, 2002). Our study answered the following research questions: what are the observed local climate changes and impacts on biophysical systems? What adaptation strategies are adopted by local people in response to global change impacts on their livelihoods? What are the indirect impacts of climate change on biodiversity?

Materials and methods

Study site

The 4,600 km^2 Lac Télé Community Reserve (hereafter the Reserve) is a Category VI protected area (i.e., a protected area with sustainable use of natural resource according to IUCN, Dudley et al., 2008). It is managed by the Congolese Ministry of Forest Economy and the Wildlife Conservation Society (WCS). It is characterized by high micro-habitat variability, including swamp forests, seasonally inundated forests, seasonally inundated savannas, riparian forests and patches of *terra firma* forests (Poulsen and Clark, 2002). It is located in the Cuvette centrale, where the largest tropical peatland complex is located (Crezee et al., 2022). The Reserve experiences 1600-1800 mm of rainfall and an average temperature of 25.6°C (Bondeko et al., 2016). The area has a bimodal rainfall pattern (Supplementary material), with a long dry season (December-March), a short rainy season (April-May), a short dry season (June-July) and a long rainy season (August-November). The Reserve exhibits pronounced seasonal hydrological fluctuations, with significant changes in water level in the Sangha, Oubangui and Likouala-aux-herbes rivers and their tributaries (Rainy & Twagirashyaka, 2010). However, the site's flooding regime, while being a key driver of ecosystem dynamics (e.g., peat formation or nutrient cycling) is poorly known (Hawthorne et al., 2023; Ifo et al., 2019). The Reserve supports over 350 species, diverse herpetofauna (e.g. the African dwarf crocodile *Osteolaemus tetraspis*), as well as important populations of central chimpanzee (*Pan troglodytes troglodytes)* and of critically endangered western lowland gorillas (*Gorilla gorilla gorilla,* Poulsen & Clark, 2004). The Reserve has approximately 20,000 inhabitants distributed in 31 villages, predominantly consisting of Bomitaba people of Bantu origin, along with minority hunter-gatherer groups such as Ba'Aka and Bakouyou communities (Faustin et al., 2007; Moukouyou et al., 2015). It has a low estimated average human population density of 3.8 inhabitants/km^2 (Bondeko et al., 2016). Local communities have developed a varied activity portfolio, relying on rainfed subsistence agriculture (cassava being the main staple), fishing, subsistence hunting (using traps and sometimes guns) and collection of non-timber forest products (NTFP). In some villages with better market access, cocoa is also cultivated for commercial purposes. Traditionally, farming and fishing are the main activities during the long dry season while hunting is practiced mostly during the long rainy season, when most seasonally flooded forests are inundated. There is no access to electricity or health centers in any of the villages studied, and the main market town is Epena (the Reserve entry point, Figure 1). Due to its isolation, deforestation trends in the

Reserve were estimated at 1.3% in 2000-2023 (WRI, 2025). Decreasing trends in abundance of large mammals and certain fish species have been reported (Ndzana Biloa et al., 2024; Poulsen & Clark, 2004).

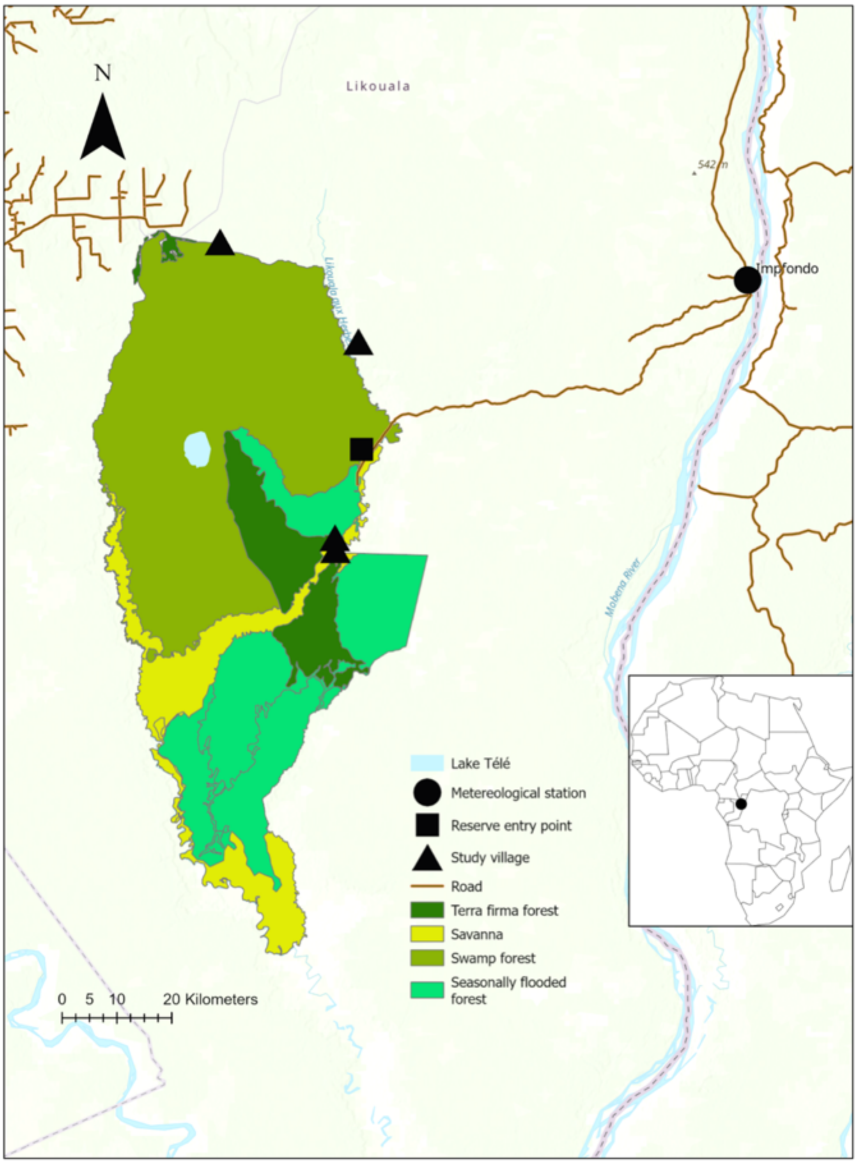

Figure 1: Map of the Lac Télé Community Reserve. Data source: WCS.

Ethics

Research activities were authorized by the Congolese Ministry of Higher Education, Scientific Research and Technological Innovation, and data collection protocols received approval from the University of Sapienza Ethics Committee for Transdisciplinary Research (ID 9/2022). Explicit consent for conducting research activities was sought through local administrative and customary leadership. Free, Prior, and Informed Consent (FPIC) protocols were upheld during the entirety of the field work. Participants were informed that participation was voluntary, and that anonymized data would be used for analysis and publication. They signed a consent form acknowledging the research objectives and those who were unable to read provided oral consent. Village chiefs and community members were informed of their opportunity to participate in the decision-making process regarding the organization of research activities. A benefit sharing mechanism was discussed in villages: in many instances, leadership requested a non-academic activity report in French after fieldwork completion.

Data collection

We selected four villages to represent habitat variability and market access: swamp forests (village 1), *terra firma* forests with market access (village 2, which had cocoa farms), seasonally flooded forests (village 3) and *terra firma* forests without market access (village 4, Figure 1). All selected villages had less than 300 inhabitants, ensuring that the integration of M.B. and C.M.M. was feasible, and were mostly inhabited by Bomitaba communities, with Ba'Aka families present in village 2. We adapted data collection methods from the standardized protocol developed by Reyes-García et al. (2023b) for the project "Local Indicators of Climate Change Impacts" (LICCI). The data collection protocol in each village included four steps: exploratory focus group discussions (FDG), semi-structured interviews, FDG validation and a quantitative survey (Figure 2).

1) Exploratory focus group (participants n=15-20)

- Focus groups were organized upon arrival in each village;
- Using open-ended questions, we guided a discussion on livelihood practices, the village's seasonal calendar and its historical timeline (including significant events such as past hazards or infrastructure development). This allowed a preliminary understanding of changes at play;
- We used a convenience quota sampling associated with gender (male/female), age (30-50/50-90 years old) and livelihoods (farming/fishing/hunting/non-timber forest product collection). After dividing village population in gender, age and livelihood quotas, we selected participants based on availability and interest, and in discussion with village leadership;

2) Semi-structured interviews (n=20)

- Using preset open-ended questions, we conducted semi-structured interviews;
- Semi-structured interviews were used to collect observations of change recorded by local communities. In this context, "observation of change" refer to indications of change in the local climate and biophysical system;
- A significant event widely recognized in the village was used as a common historical reference point to delineate changes;
- We used a convenience quota sampling associated with gender, age and livelihood groups (see step 1). We included a minimum of 3 participants per quota, depending on the saturation of information;
- We aimed at including individuals that had not participated in previous research activities;
- Participants had a minimum of 30 years.

3) Second focus group (participants n=15-20)

- We organized a second focus group to present and validate data collected during the semi-structured interviews, generate an exhaustive list of observations of change and gather additional contextual data;
- We used a convenience quota sampling (similar as step 1);
- We aimed at including individuals who had not participated in previous research activities.

4) Quantitative survey (n=29*)

- With closed questions, the quantitative survey aimed at assessing the extent of the adoption of adaptation measures in each village;
- We established, on site, a list of adopted adaptation strategies, adjusted to the village context, based on results arising from the previous steps. Therefore, it resulted in variations from a village to another;
- We used a stratified random sampling integrating livelihoods and gender. After dividing village population into each strata, we applied a random selection to select participants. We reiterated the process if selected participants were not available;
- We aimed at including individuals that had not participated in previous research activities.

* Although we aimed to conduct 29 quantitative interviews per village, the actual number varied slightly based on the local context (village 1 n= 29, village 2 n= 24, village 3 n=29, village n=29).

Figure 2: Graphical representation of the methodological approach used in in each village, adopted from (Reyes-García et al., 2023b).

All interviews were conducted in an oral format. The Lingala language was used in most interviews and FDG, with occasional use of Bomitaba terms; responses were translated into French by C.M.M. In village 2, 19 interviews were conducted in Ba'Aka, with the assistance of an additional interpreter who translated participant response from Ba'Aka into French. In total, 191 interviews and 8 focus group discussions were conducted (see the Supplementary material for questionnaires used). In all villages, additional contextual observations associated with reported climate change impacts on the local biophysical system or with adaptation strategies adopted by local communities were collected by M.B and C.M.M while accompanying study participants in daily subsistence activities (including farming, fishing, NTFP gathering and cooking). Monthly maximum, mean and minimum temperature and monthly rainfall data from the Impfondo meteorological station (for the period 1990-2023) were obtained from the National Civil Aviation Agency of Congo.

Data analysis

We used villages as the main unit of analysis. To investigate observed changes in the local climate and impacts on the Lac Télé Community Reserve biophysical system, we translated interviews into English and created codes for each respondent, following this format: village number - female/male – individual number. We translated each change observation into a standardized indicator with directional change (e.g. "*decreased fog intensity*"), assigned each indicator to the atmospheric, biophysical or human system (following Reyes-Garcia et al., 2023b), and counted the total number of citations (per village and across all villages) of indicators. We removed indicators not validated by at least one FDG (n=7 not validated). We performed linear regression analyses on meteorological data, using monthly mean, minimum and maximum temperature, monthly rainfall values and 10-year running mean as dependent variables and the time series as the independent variable. We applied mean imputation (i.e. replacing missing values with yearly average) to fill data gaps; years with data gaps exceeding four months were excluded from the time series (n=1 for mean temperature, minimum temperature and rainfall, n=4 for maximum temperature). To investigate decadal changes in seasonal patterns, we displayed temperature (minimum and maximum) and rainfall in each of the four seasons (long dry season, short rainy season, short dry season and long rainy season). To assess adaptation strategies adopted by Lac Télé Community Reserve inhabitants and potential indirect impacts on biodiversity, we classified study participants according to their self-identification of main personal subsistence activities: farming (n=113), fishing (n=86), hunting (n=28) and NTFP collection (and affiliated activities). The latter was further disaggregated into subcategories (edible plant collection, n=54, *Raphia* spp. collection for house construction and basketry, n=39, wild honey collection, n=34, and dugout canoe construction, n=33). Then, we used descriptive statistics to evaluate the distribution of the adoption of adaptation strategies among the surveyed groups. We classified the adaptation strategies reported by respondents according to potential impacts on biodiversity, following a classification derived from the IPBES-IPCC co-sponsored workshop on biodiversity and climate change, which considers the following categories: "*biodiversity positive*", "*biodiversity neutral*", "*biodiversity possible risk or benefit*" and "*biodiversity negative*" (IPBES-IPCC, 2021). In the manuscript, words and species names in Lingala or Bomitaba language are recorded using brackets. We performed a paired t-test to determine if the responses of the Ba'Aka respondents differed significantly from those of the Bomitaba respondents within the same village. As the results did not show significant difference between the two groups (Supplementary material), responses from both ethnic groups were combined in the Results section.

Study limitations

Our study approach has certain limitations. First, we only studied four villages per ethnic group. In our study area, biophysical or socio-economic differences among the villages of one ethnic group are rather limited (e.g., market access or the presence of external change agents). Then, indicators of change reported by local communities may have been influenced by the extreme flooding event (at the time of data collection), potentially biasing observations towards an emphasis on floodings while underrepresenting other possible indicators. Responses related to hunting and fishing activities may have been influenced by hesitancy to discuss them in detail, since these activities are restricted within the Reserve. Furthermore, while our primary focus is on climate change, adaptations to climate change are likely influenced by other drivers of change, such as rising costs of living. We were unable to obtain detailed information on adaptation responses related to cocoa farming, which should be investigated in future work. We acknowledge that the necessary use of translation from Lingala to French, as well as from Ba'Aka to French, may have influenced the transmission of concepts and nuances expressed by study participants.

Results

Meteorological data

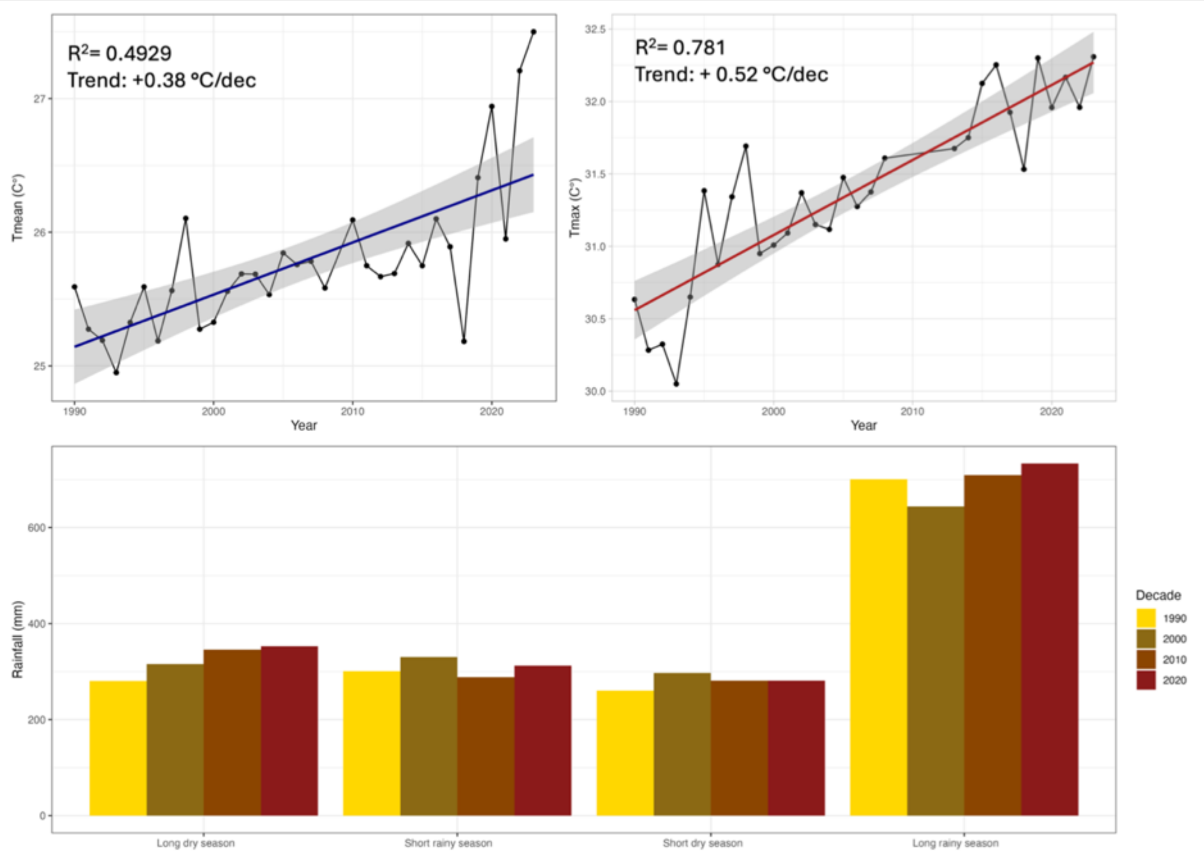

Figure 3: Linear trend of annual mean temperature (top right); linear trend of annual maximum temperature (top left); decadal seasonal rainfall (bottom) at the Impfondo meteorological station. Data source: Agence Nationale de l'Aviation Civile du Congo.

During the 1990-2023 period, our linear regression analysis indicates a statistically significant increase of annual mean temperature of 1.29°C (± 0.007 SE, $p < 0.001$), corresponding to 0.39°C (± 0.007 SE) per decade. Annual maximum temperature showed a larger increase of 1.71°C during the same period (± 0.005 SE, $p < 0.001$). The seasonal temperature evaluation based on the 10-year running mean showed a significant, but small increase of minimum temperature in the long dry season (0.13 °C, ± 0.014 SE, $p < 0.05$) and short rainy season (0.55°C, ± 0.059 SE, $p < 0.05$), and maximum temperature during the short rainy season (0.27 °C, ± 0.05 SE, $p < 0.05$) and long rainy season (0.47 °C, ± 0.07 SE, $p < 0.05$). Regarding rainfall, no significant trend was observed in annual average during the total period (Supplementary material), but a small increase of 26.4 mm (± 0.46 SE, $p < 0.05$) per decade was found in the long dry season based on the 10-year running mean.

Observations of change in the local atmospheric, biophysical and human systems

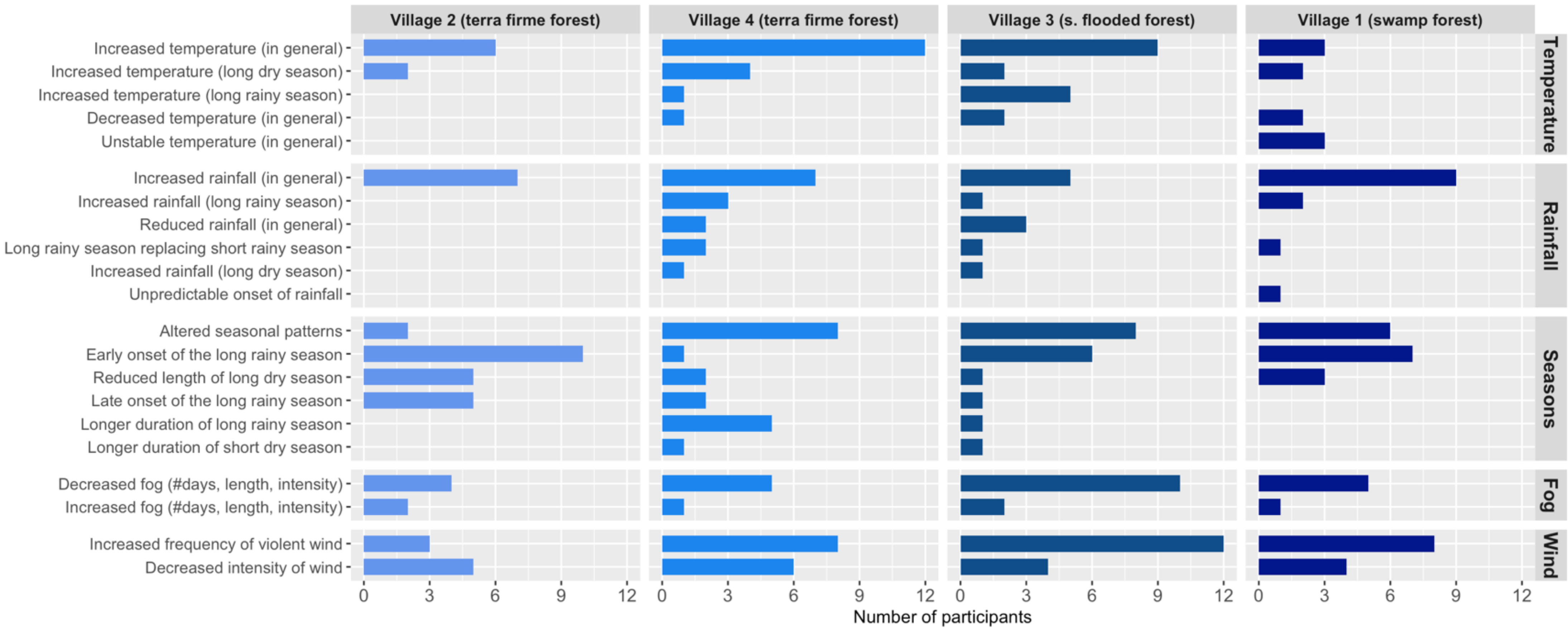

Figure 4: Indicators of change reported by respondents in the atmospheric system, n=20 respondents per village. Villages ranked according to flood impacts (see Supplementary material for additional details on indicators).

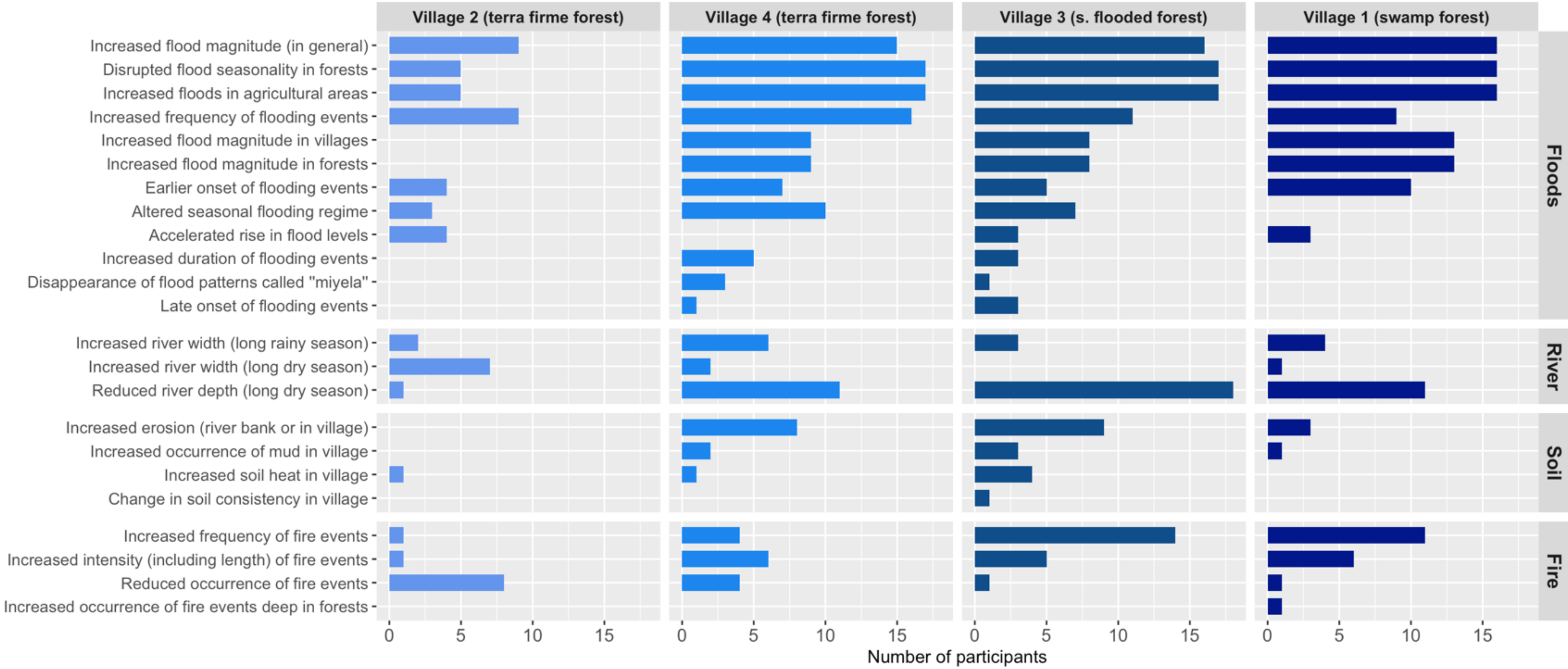

Figure 5: Indicators of change reported by respondents in the biophysical system, n=20 respondents per village. Villages ranked according to flood impacts (see Supplementary material for further details on indicators).

In total, respondents reported 364 indicators of change: 25 in the atmospheric system, 295 in the biophysical system and 44 in the human system (Supplementary material). In the atmospheric system (Figure 4), most of the indicators of change reported pertained to increasing temperature (n=30), specifically during the dry season (n=10) and increased (n=28) disrupted rainfall distribution (n=18). Twenty-four respondents reported a decrease in fog intensity during the dry season. Respondents reported significant shifts in the flooding regime. They described an increased occurrence of floods of magnitude and duration previously unexperienced (n=56). Whether in villages, agricultural fields or forested areas, water levels were described as the highest recorded in human memory ("*the whole village has been flooded,* [and] *up to 45 km or even 60 km into the forest is accessible by pirogue* [...], *the entire area is flooded*", 1-M-1). Thirty respondents highlighted that the floods penetrated deeper into the forests than previously observed. Respondents reported disrupted seasonal flooding patterns (n=20), with an onset in March instead of September (n=26). Although the floods occurred early, their extent in September was unusually low, specifically in forested areas. Respondents described a significant decrease in the depth of the Likouala-aux-herbes river during the dry season (n=41 respondents), one declaring "*the river has changed; it used to be deep, but it's not anymore*" (3-M-11). Increased soil erosion (n=20) was described "*as if the ground is changing, it is leaving, the erosion is pulling the earth; in one plot, a palm tree fell into the water, it is dangerous*" (1-M-19). Another noted: "*in my opinion, the soil is breaking up because it was under* [flood] *water, and with the heat of the [mwanga]* (dry season)*, it dries out, it breaks up and erosion progresses*" (3-F-18). Thirty respondents mentioned an increased frequency of fire events (attributed to both changes in fire management practices, such as reduced adherence to traditional methods, and rising temperatures) while 18 others also described an increased intensity (including length) of fire events. Increasing fire events were associated with the disappearance of gallery forests (n=33 respondents) and encroachment into the forest periphery (n=22), identified as one of the most substantial changes in the landscape. One respondent said: "*the forests along the river have disappeared in front of my very eyes. In times of drought, they burn and burn and burn*" (4-F-10). The annual hydrological cycle exerts a strong influence on people's livelihoods, and, historically, local communities have developed a seasonal activity portfolio adapted to floods (M.B., personal observation, also see Supplementary material - Fine-scale human-flood relationships in the Congo Basin: Ethnographic perspectives from the Lac Télé Community Reserve). With disrupted flood patterns, respondents reported wide-scale impacts on their livelihoods and well-being. In 2023, agricultural fields were flooded in all villages studied, including areas typically not subject to severe flooding, and near-total crop loss in others. A respondent declared: "*I harvested cassava with water up to my chest* [...] *I had to plunge my head into the water. We suffered a lot.* [...] *I had to harvest early, because normally floods* [pela] *arrive in November, and that is when we harvest.* [...] *I have lost my three fields*" (3-F-7). In one *terra firma* village, only 13% of fields (Supplementary material) were affected, but this was also considered alarming, given that such floods had never occurred there before. One respondent stated: "*we saw fish in the cocoa fields* [for the first time]" (2-M-2). In village 1, the untimely floods also caused a disruption of the main fishing season and a loss of income for 57% of respondents. In village 3, 83% of respondents reported a decrease in food availability due to the extreme floods, and 63% reported increased cases of the African cassava mosaic virus.

Observations of change linked with Lac Télé Community Reserve biodiversity

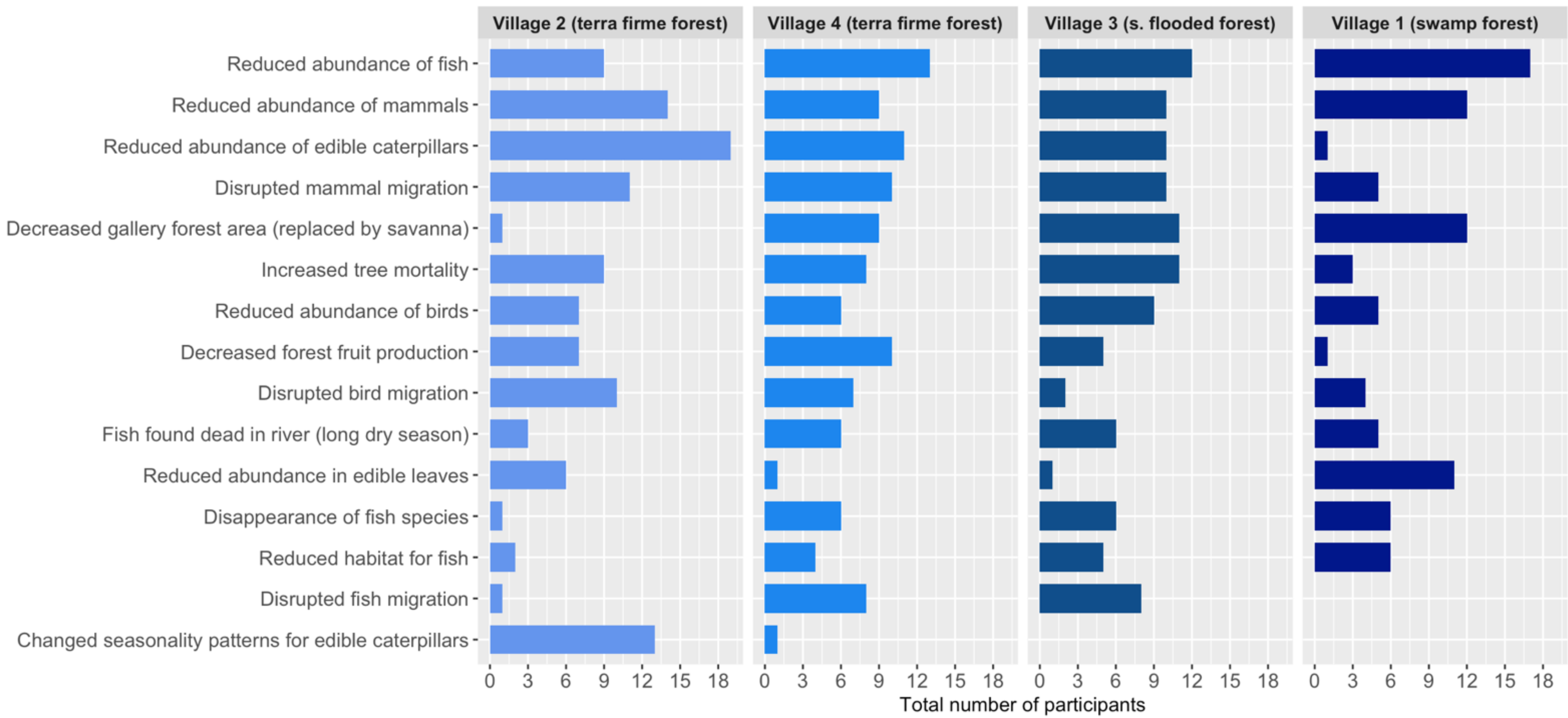

Figure 6: Summary of the 15 most observed indicators of biodiversity change in Lac Télé Community Reserve biodiversity, n=20 respondents per village. Villages ranked according to flood impacts (see Supplementary material for further details on indicators).

Overall, the indicators of change related to fish (n=121), plants (n=73), mammals (n=64), caterpillars (n=55) and bird species (n=47) were the most common (Figure 6). Respondents depicted multifaceted impacts of climate change on fish populations. A commonly expressed opinion was that floods of large magnitude usually have a positive effect on fish reproduction and stocks (n=11 respondents). Respondents declared that "*water is like a village for the fish" (3-M-15)* and "*the fish reproduce well when the water goes far into the forest and enters ponds*" (4-F-9). However, respondents mentioned being perplexed by the impacts of disrupted cyclicality on fish stocks. One person stated: "*the fish weren't able to enter the forest at a time when they should normally be there, normally the second half of October* [...] *so they are waiting in the river*" (4-M-8). There was disagreement between villages regarding the reproduction success of fish species amidst flood disruption. One group (village 3) stated "*in the same way that we humans were surprised by the water, the fish were too. In April, we didn't see the youngs of the* [moungoussou] (Parophiocephalus obscurus). *In April, the fish had no eggs in their abdomens. The eggs were seen in the bellies of the fish when the water level dropped* [...]. *The fish are disturbed*". Another group declared "*we don't know whether the fish are reproducing, perhaps we'll have to wait until the dry season to find out.* [...] *we don't really know to what extent they have been disturbed*" (village 2). Moreover, respondents (n=20) mentioned the more frequent occurrence of floating dead individuals during the long dry season, frequently citing [moungoussou] *(Parophiocephalus obscurus).* Respondents reported a significant increase in tree mortality due to the effects of extreme floods (n=30). Tree species adapted to *terra firma* habitats or to regular seasonal flood cycles were identified as vulnerable to prolonged exposure to water, e.g. [eyeyi] (*Macaranga brunensis*). Recruitment rates were also considered to be negatively affected by changing flood patterns, with observations including tree seedlings in *terra firma* habitats. In addition, we recorded 23 observations of reduced fructification of several species, [malombo] (*Saba senegalensis*) being the most frequently mentioned (n=17). The effects of increasing dry season duration or intensity on plant species were also discussed. One respondent mentioned: "*it's too hot nowadays, it even stings the skin. The leaves on the trees are thinning* [i.e. reducing in abundance]*, even the fruits* [are] *thinning, even the Raphia palm fruits* [mbila] *are small. The fruits* [in the village] *don't reproduce well. The orange trees have disappeared because of the heat*" (3-M-11). Respondents also emphasized the effects of floods on altered migratory patterns for mammal species (n=36 respondents). In 2023, the altered pattern and increased duration of annual floods appeared to disrupt typical migratory patterns, rendering, in some cases, the usual response ineffective. One respondent stated: "*you could say that the animals are disturbed;*

some cannot tolerate water. Small duikers [mboloko]*, hedgehogs* [ngoumba] *flee to find dry land. [...] They endure or go elsewhere like men. Each year, they adapt. Before, the forest didn't flood like it does now. It was just in the corners. It's difficult for them too"* (4-M-4). Increased abundance of *Gorilla gorilla gorilla* was reported during the flooded period near village 2 (*terra firma* forests): "*before, when I went fishing, I didn't see many gorilla nests. This time, there were a lot, and I was even scared to go fishing.* [...] *Maybe because they've had lots of youngs or they've fled because of the water in search for food*" (2-M-5). Increased mortality among small- sized species, for which long-distance displacement is more challenging, was also reported, although infrequently (n=2, focus group agreement): "*I have seen 16 dead porcupines. They probably got stuck and ran out of food*" (2-M-23). Increased heat was also described as a concern for mammals: "*the sun* [...] *is difficult for animals too. When the heat is too much, the animal will be bothered. If the sun breaks through and gets to where he is, it will push him to go somewhere else where it's cooler to rest*" (3-M-9). The alteration in flood timing appears to affect migratory bird population (respondent n=23). Marabout storks (*Leptoptilos crumenifer*) were reported to arrive in large groups during the dry season, exploiting shallow water bodies to feed on small fish. A respondent observed that "*the storks [marabouts] arrive in March,* [...] *they come to eat the fish.* [...] *They didn't eat much because the dry season* [mwanga] *didn't go all the way, [they] left just afterwards*" (2-F-11). Reduced food source was also identified as a problem for other bird species such as the heron [mwangalaka] (*Ardea purpurea*/*Ardea melanocephala*) and the African drafter [edi-edi] (*Anhinga rufa*) (n= 5). Other observations mentioned less frequently include reports of damaged reptile eggs (n=2, focus group agreement), asynchrony between reptile species' reproductive strategies and flood timing (n=1) or the effect of increased heat on reptile physiology (n=1).

Figure 7. 1) Fallen trees resulting from extreme flood-induced impacts; 2) The Likouala-aux-herbes river becomes large during extreme floods; 3) Flooded village; 4) Gallery forest fire ; 5) Flooded *terra firma* forest.

Local communities' adaptation measures

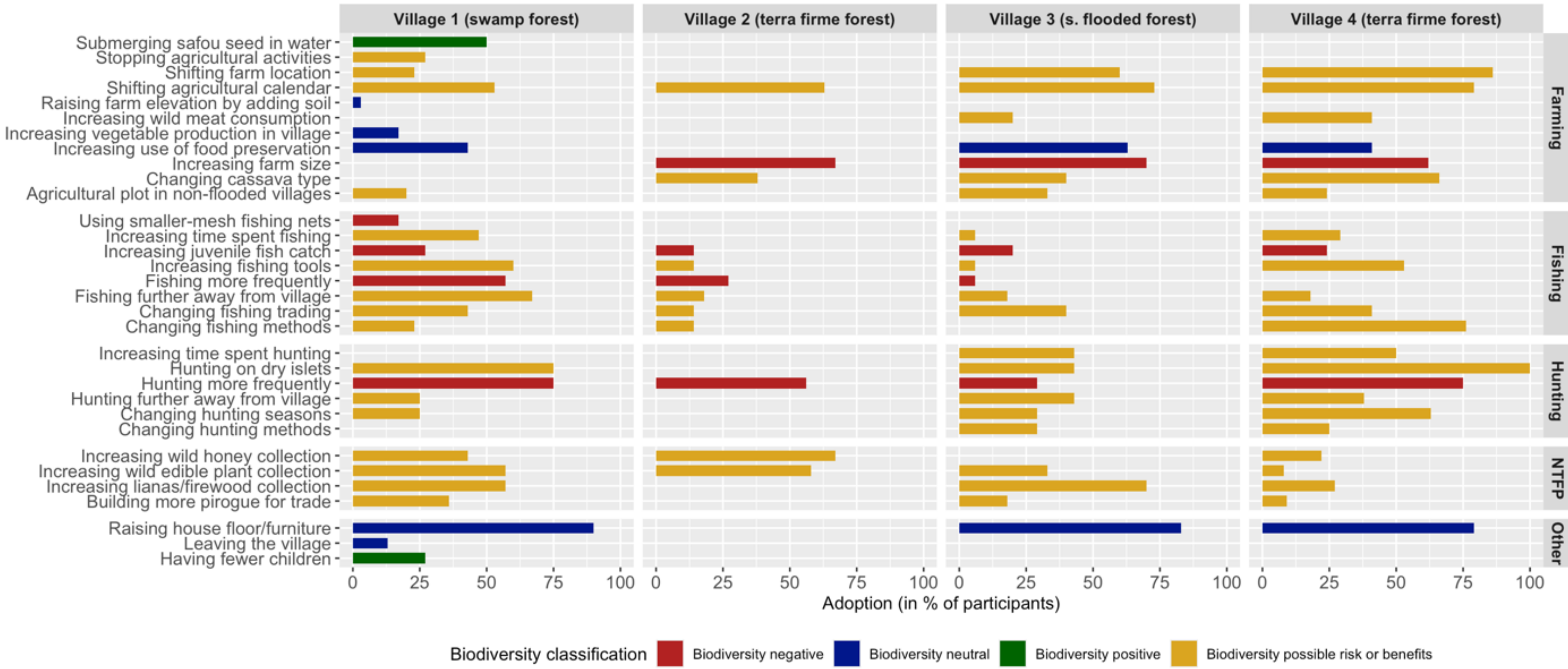

Figure 8: Adoption rate of reported adaptation measures across villages and potential indirect impact on biodiversity (n=111). Villages ranked according to flood impacts.

Our respondents reported 32 adaptation responses, with variability across villages (Figure 8). Adaptations related to all subsistence activities (farming, fishing, hunting and NTFP collection), shelter or living strategies (e.g., reproduction and migration to other Reserve villages). The most recorded responses included shifting agricultural calendars, increasing fishing material or hunting more frequently. Other adaptation measures, such as permanent emigration or having fewer children, were only considered in one of the most flood-affected village. Most adaptation measures were linked to flood impacts on respondents' livelihoods, although many were concomitantly associated with other factors (e.g. reduced fish stocks). In the agricultural sector, shifting agricultural calendars were reported in all villages (from 53% in village 1 to 79% in village 4). Most respondents (e.g. 70% of the respondents in village 3) reported increasing agricultural surface, a respondent noting "*I need to make a bigger field on dry land, because it doesn't flood*" (3-F-2). Some respondents also relocated agricultural fields to previously unexploited *terra firma* forests, especially in village 4 (86%), where local authorities decided to allocate a portion of previously unused forested land to agriculture to mitigate the impact of floods on crop yields. In areas where *terra firma* forests were not easily accessible, villagers moved agricultural activities to locations less affected by floods, such as small higher elevation zones. Increased heat during the dry season led villagers to advance their planting dates, which was viewed as a measure to counter African cassava mosaic virus. It also prompted villagers to increase agricultural efforts, for example by expanding the number of fields: "*before, our parents only did the fields once, but now we have to do it twice because of the disease*" (3-F-10). We noted variations in adaptation responses related to fishing depending on villages. In village 1, where floods severely affected crop yields, there has been a subsistence shift towards fishing: 53% of respondents reported an increase in fishing efforts; 67% practiced fishing in new forested fishing grounds made accessible through the high flood levels; and 60% of respondents increased fishing material. Village 1 also had the highest juvenile fishing catch report, and many residents reporting an increased proportion of their fishing efforts dedicated to sales (%): "*the share of sales has changed; you have to buy more cassava because there are no fields* [anymore]*; the floods has changed* [our] *management*" (1-F-21). In other villages, where agriculture plays a more prominent role, the focus on fishing in response to floods was less pronounced. Villagers prioritized preserving cassava production over increasing fishing efforts. Still, a respondent in village 3 indicated that '*the disruption caused by the* [untimely] *floods in the forest gave an advantage* [...]*". Because flood occurrence increased, fishing is encouraged, and young people have been able to go more into the forest to [fish]*' (3-M-7). Regarding hunting, changes in frequency and in period of the year were most reported, followed by hunting further away or for a longer period. In village 1, 75% of respondents reported more frequent hunting compared to a typical flooding season (October-November), e.g. because flood levels facilitated pirogue-access to more remote forested areas. In village 4, a respondent stated: "*this year* [2023], [the floods] *rose very strongly* [...] *hunting was easy*" (4-M-11). Several respondents, however, reported ceasing hunting activities during periods of excessively high or rapid flooding, as it made walking in forest more difficult and rendered certain techniques, such as using traps, impractical. Several others reported a decreasing interest in hunting activities, regardless of the potential increased success rate driven by high flood levels, citing their arduous nature, the discouraging presence of eco-guards and the higher profitability of other subsistence activities (including fishing), considering the costs of material such as cartridge. A variety of other activities related to NTFP collection was also affected, some even becoming markers of the magnitude of flood impacts. One respondent declared about the collection of *Raphia laurentii* leaves: "*I have been there three times this year, previously it was only once; the rising waters have made it easier for me to go into the forest* [using the pirogue]. *I would never have gone without* [pela] (rainy season)" (3-M-1).

Potential impacts of adaptation measures on biodiversity

Reported adaptation measures may have differential impacts on the Reserve biodiversity. Among adaptation strategies in the agricultural sector with potential negative impacts on biodiversity, we noted the expansion of agricultural surface area and shifting field location, as cropland expansion can lead to increased deforestation and land fragmentation, reducing habitat size and connectivity. Hunting and fishing more frequently also fall in that category. We identified less common adaptation measures that can positively impact biodiversity, such as enhancing intra-village agrobiodiversity by submerging safou seed (*Dacryodes edulis*) in water before planting it, with the aim of enhancing the resistance of fruiting trees to floods, or ceasing agricultural activities entirely. Approximately 62.5% of adaptation measures observed across the Reserve were categorized under the category "*possible risk or benefit*", due to the numerous mediating factors influencing its socio-ecological system. For instance, in the fishing sector, while the opening of new fishing grounds linked with the "*fishing further away*" adaptation measure could facilitate the extraction of natural resources, increased flooding may lead to a decrease in fish density, potentially reducing overall fishing pressure. Similarly, it is unclear whether "*hunting for longer*" is associated with increased catch. Traditionally, most hunting occurs during the long or short rainy season, when hunters use local topography to target animals seeking refuge in non-flooded areas. Rising flood levels may increase the hunting pressure on wildlife by driving species migration toward *terra firma* or higher elevation areas, making animals easier to catch. Many respondents recalled the year 2000 as the last time an extreme flood affected the Reserve, leading to increased hunting efforts and local extirpations of species, such as the African grasscutter (*Thryonomys swinderianus*). However, similar occurrences were not reported during recent large-scale floods. Furthermore, it seemed that several factors significantly constrain adaptation capacities in local communities within the Reserve. Many respondents simply noted "*we are just putting up with it*" (1-F-6) or "*what can we do?*" (1-F-8). This is exemplified in village 1 (swamp forests), where space for agriculture, already limited, is further diminishing due to increasing floods, and where alternative livelihood options are scarce. As a result, overall impacts on local biodiversity appear limited.

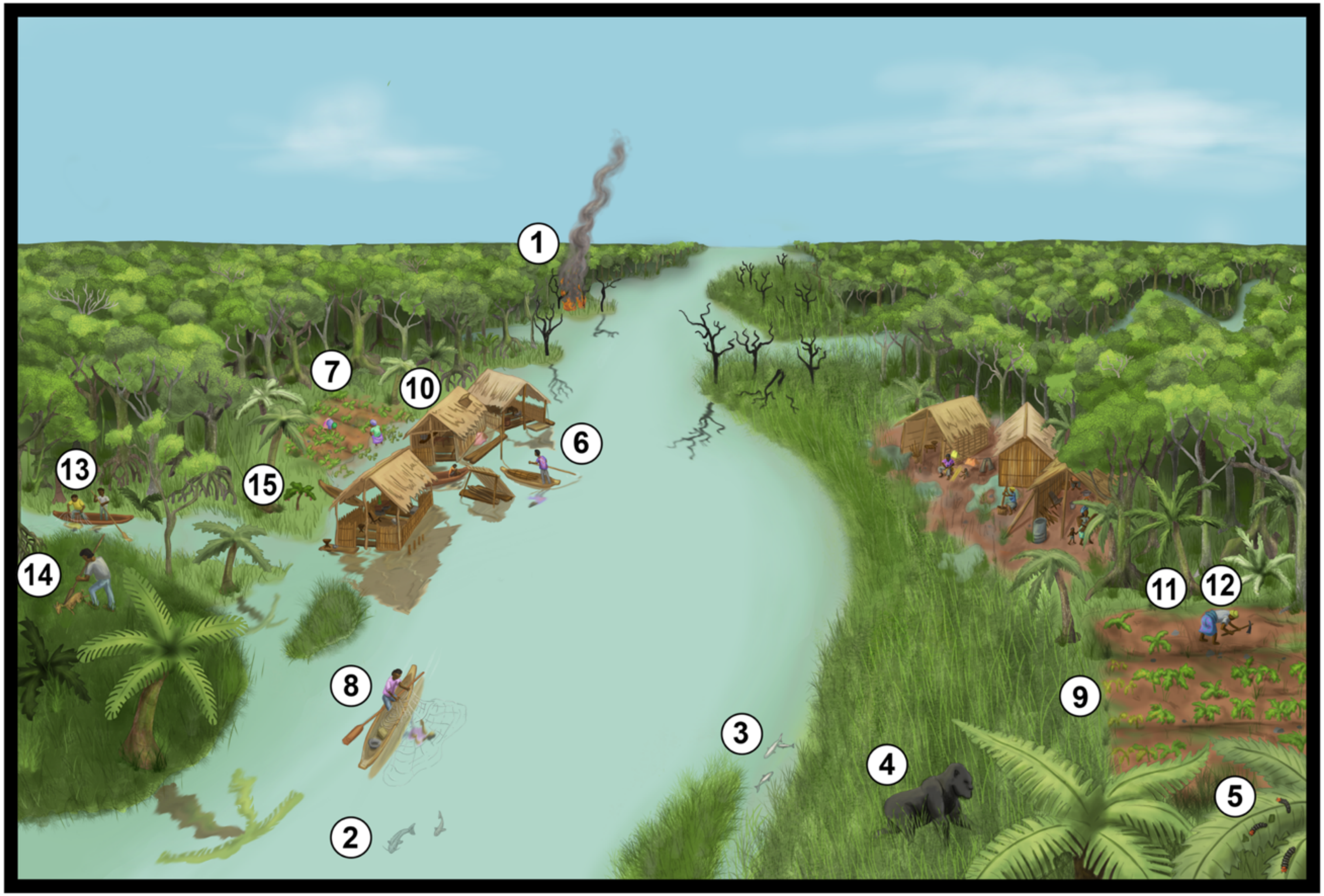

Figure 9. Visual summary of the variety of observed changes in the Lac Télé Community Reserve, including biodiversity changes, human system impacts and adaptation measures: 1) gallery forest decrease due to increasing fires; 2) reduced abundance of fish; 3) fish found dead; 4) disrupted mammal species migration; 5) changed seasonality patterns of edible caterpillars; 6) flooded village; 7) flooded agricultural fields; 8) disrupted fishing season; 9) increased cases of African cassava mosaic virus; 10) smaller quantities of food for villagers; 11) villagers shifting agricultural field location; 12) villagers increasing agricultural surface; 13) villagers shifting fishing grounds; 14) hunters using dry islets; 15) submerged safou (*Dacryodes edulis*) seed.

Discussion

Observed local climate change and impacts on biophysical systems

Local communities within the Lac Télé Community Reserve have documented a variety of climate changes, including increased temperature, changing rainfall patterns and a disrupted flooding regime. Previous literature has established a concordance between local observations of climate change and meteorological data (Savo et al., 2016). Indeed, reported changes generally aligned with existing meteorological data. For instance, increased rainfall during the long dry season, surpassing that of the short rainy season, aligned with reports of "*unrecognizable*" rainfall patterns in the Reserve. Detailed insights provided by local communities on changes in flood frequency and magnitude are particularly significant considering the paucity of instrumental records associated with water level variations, both spatial and temporal, in the Reserve studied and the broader Congo Basin (Alsdorf et al., 2016). Most climate changes reported by respondents in this study are also consistent with findings from local communities in other Congo Basin regions: while increasing unpredictability of rainfall and shifting seasonal patterns are reported in Cameroon and Equatorial Guinea (Few et al., 2017), smallholder farmers in the eastern DRC have observed increased temperatures, changing rainfall patterns, reduced fog and stronger winds (Amani et al., 2022; Batumike et al., 2021).

Respondents to our study documented several significant impacts of climate change on biophysical and human systems. These include disrupted migratory patterns of several mammal, bird and fish species; decreased production of wild fruits; reduced availability of wild edible caterpillars; increased tree mortality attributed to the change in flooding patterns; and reduced crop yields, a phenomenon frequently documented among Congo Basin smallholder (e.g., in the DRC, Amani et al., 2022 and Batumike et al., 2021; in Cameroon and Equatorial Guinea, Few et al., 2017). Increased soil erosion, floods and prevalence of the African cassava mosaic virus have also been observed in the eastern DRC, where respondents attributed the rise in disease prevalence to increased showers during the dry season (Amani et al., 2022). In the Reserve, increased disease prevalence was associated with elevated temperature and heightened flood exposure. Although we were unable to identify local observations of changes in species migratory patterns in other Congo Basin seasonally flooded systems, our findings are consistent with ecological studies in the Amazon. In line with reports from study participants, seasonal flooding is identified as a significant driver of migration for Amazon floodplain species, with mammals employing strategies such as retreating to higher elevation refuges, temporarily migrating to unflooded areas or using arboreal pathways within the forest midstory or canopy to cope with periodic flood disturbances and associated habitat and food resource reduction (Ramalho et al., 2021). Amazon fish migrations are also closely related to seasonal floodings, with increased flood extent and duration enhancing habitat availability, food resources and recruitment opportunities (Castello et al., 2019). However, extreme flooding events can adversely affect fish communities, particularly when accompanied by changes in flood timing (Chea et al., 2020). In the Congo Basin, local communities located outside seasonally flooded systems, such as in the eastern DRC, have reported reductions in wild fruit production and availability of wild edible caterpillars related to climate change (Batumike et al., 2021). Similar declines in edible caterpillars have been observed in Cameroon, attributed to both climate change and logging activities (Ngute et al., 2020). If widespread across the Reserve and the broader Congo Basin region, a reduction in wild fruit production could have significant consequences not only for human populations that consume and trade these resources, but also for species reliant on fruits (Bush et al., 2020b), including *Gorilla gorilla gorilla* found in the Reserve (see for example Masi et al., 2009, 2015, and Robira et al., 2023, on the influence of fruit availability on *Gorilla gorilla gorilla* foraging strategy, movements and activity budget). In Gabon's Lopé National Park, a dramatic 80% reduction in wild fruit production over a 32-year period has been linked to reduced body mass in African forest elephants (*Loxodonta cyclotis*, Bush et al., 2020b). This severe decline in fruit production has been further associated with an increase in minimum decadal temperatures, which was also observed in the Reserve.

Adaptation strategies

Study participants reported 32 adaptive strategies related to farming, fishing and hunting practices, as well as in-house adaptation. Certain strategies, such as increasing farm size, were driven by a combination of factors, including reduced crop yields, but also rising costs of living. Expanding farm size and diversifying off-farm activities were also documented in the eastern DRC (Batumike et al., 2021), though that study did not focus on seasonally flooded systems. Notably, in contrast to other studies (e.g. in Cameroon or the DRC), we did not observe a pronounced increase in NTFP reliance as a safety net against climate-induced crop failure (Da Cunha Ávila et al., 2021). This may be due to the high baseline reliance on NTFP in the communities studied, as suggested by Batumike et al. (2021). Several adaptation responses observed in the Reserve are also reported in studies of floodplain local communities in the Amazon. For example, strategies such as harvesting crops in waist-deep water, elevating household items onto platforms and submerging sealed cassava bags in water for preservation were also noted by Da Cunha Ávila et al. (2021). Interestingly, these authors documented additional biodiversity-friendly adaptations, including constructing stilt houses, using floating boards for agriculture and minimizing stress on fruit-tree root systems, which were not mentioned by our study participants. Given their biodiversity-friendly nature, these practices could be considered in future discussions with Reserve local communities, as highlighted in the section below. Those considerations are supplemented in an ethnographic study entitled "*Fine-scale human-flood relationships in the Congo Basin: ethnographic perspectives from the Lac Télé Community Reserve*", which provides an in-depth exploration of local communities' understandings of and adaptations to hydrological processes in the the Lac Télé Community Reserve (Supplementary material).

Adaptation measures' potential impact on biodiversity

We found that 62.5% of adaptation strategies reported by respondents can be classified as "*possible risk or benefit*" for biodiversity, as their impacts are influenced by various factors. For instance, expanding farm size may negatively impact biodiversity if it involves clearing old-growth forest rather than fallow land. This highlights the necessity for continued monitoring of Reserve local communities' adaptation strategies to more effectively identify those that are biodiversity-friendly. One potential approach could involve examining biodiversity-friendly strategies used in other regions, such as Amazon floodplain ecosystems, to assess constraints and opportunities for their adoption. It is important to note that we did not evaluate the effectiveness or sustainability of the strategies reported by the respondents. Rather than recommending best practices, the range of adaptation responses documented here can serve as a basis for identifying potential approaches for testing in other seasonally flooded areas of the Congo Basin, particularly those that are biodiversity-friendly.

Implications of the findings

The statement "*we saw fish in the cocoa farm*", expressed by one of our respondents, highlights the profound severity of climate change impacts and increasing livelihood constraints in an already isolated Congo Basin rainforest context. Such impacts may reinforce challenges to biodiversity conservation within the Lac Télé Community Reserve. This situation likely reflects the realities of many seasonally flooded sites across the region. To effectively reconcile biodiversity conservation and local development objectives in this ecologically critical area, a comprehensive understanding of climate change impacts on both biodiversity and livelihoods is of crucial importance. Indeed, the Congo Basin is projected to experience more extreme floods (Bola et al., 2022; Tshimanga et al., 2016) and droughts (Karam et al., 2022), but the monitoring of climatic variables (Yakusu et al., 2023) and of climate change effects on biodiversity remains insufficient (Beekmann et al., 2024). As our study demonstrates, local communities can offer valuable insights into the fine-scale impacts of climate change. Our study facilitates an improved understanding of ongoing changes and also contributes to filling an important data gap linked to IP&LC adaptation strategies in Central Africa. Crucially, an interrogation remains: how to strengthen the resilience of local communities to climate change impacts, without compromising biodiversity conservation objectives? Addressing such a question will benefit from enhanced co-production of knowledge among stakeholders, prioritizing "*science with society*" over "*science for society*" approaches (Steger et al., 2021). This inquiry is vital for the future of the Lac Télé Community Reserve and other floodplain socio-ecosystems within the Congo Basin.

Chapter IV

Shrinking climatic space: Implications for forest elephant conservation in the Congo Basin under climate change

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Abstract

The African forest elephant (*Loxodonta cyclotis*), a keystone species in Afrotropical rainforests, plays a critical role in maintaining forest structure, seed dispersal and ecosystem dynamics. In addition to the well-documented pressures of ivory poaching and deforestation, climate change is also emerging as a significant threat. While climate change has been linked to altered migration patterns and increased mortality of the African savanna elephant *(Loxodonta africana)*, its effects on *Loxodonta cyclotis* remain understudied. This study employs a bioclimatic envelope modeling framework coupled with an ensemble forecasting approach to assess projected shifts in the species' climatic niche under a business-as-usual (medium greenhouse gas emission, SSP 245) and worst-case (high emissions, SSP 585) by 2100. Considering sampling biases associated with forest elephant occurrence points, we also generated pseudo-presences by sampling along a regular grid within the forest elephant geographic range. By contrasting the two occurrence datasets, we aimed to assess the extent of

future climatic suitability predictions for the forest elephant. Our results indicate a consistent contraction in climatically suitable habitats, particularly in the central Congo Basin, with increasing fragmentation in West Africa. Crucially, projections suggest that a significant proportion of current protected areas will lose climatic suitability, raising concerns about the effectiveness of existing conservation frameworks. Furthermore, regions projected to retain favorable climatic conditions are also projected to be at high risk of deforestation. Our findings underscore the need to expand protected areas to include projected climate refugia and explore alternative conservation approaches, such as sustainable land-use planning in logging concessions. Our research seeks to contribute to a deeper understanding of how climate change impacts one of Africa's most iconic species, informing conservation policy for *Loxodonta cyclotis* under shifting climatic conditions.

Introduction

The African forest elephant, *Loxodonta cyclotis* (Matschie, 1900), member of the Elephantidae family, was recognized as a distinct species in 2021, based on genetic, morphological, behavioral and ecological studies (Groves et al., 2000; Ishida et al., 2011; IUCN, 2024). Smaller than the African savanna elephant (*Loxodonta africana*), the African forest elephant (thereafter, forest elephant) also live in much smaller groups, with an average core group size of 2.8 individuals, often composed of mothers and their dependent offsprings, and operating under a fission-fusion social structure (Brand et al., 2020; White et al., 1993). The forest elephant is a generalist herbivore, with daily consumption reaching up to 150 kg of vegetation per day, including fruits, barks and leaves (Berzaghi et al., 2023; Blake & Maisels, 2023). While the forest elephant movement ecology has long been unexplored, home range size estimates vary between 25 km^2 to more than 2,200 km^2 (Blake & Maisels, 2023). Forest elephant range countries include Benin, Burkina Faso, Côte d'Ivoire, Ghana, Guinea, Guinea-Bissau, Liberia, Niger, Nigeria, Senegal, Sierra Leone and Togo in West Africa, and Cameroon, the Central African Republic, the Democratic Republic of the Congo (DRC), Equatorial Guinea, Gabon and the Republic of Congo in Central Africa (IUCN, 2024). The estimated total population of forest elephants is approximately 133,300 (95% CI 97,000-169,890, CITES, 2022).

As the largest forest dwelling mammal species in Afrotropical rainforests, the forest elephant performs critical ecological functions, acting as an ecosystem engineer and a keystone species. Through movement and browsing, by felling trees, creating permanent forest corridors and clearings, it influences forest structure, dynamics and biogeochemical cycling, facilitating habitat use by other fauna (Blake & Inkamba-Nkulu, 2004). It enriches soil nutrient by the deposition of dungs and plays a key role in seed germination and dispersal: at least 335 species, from 213 genera in 65 families, are known to be dispersed by forest elephants (Campos-Arceiz & Blake, 2011), which serve as an obligate disperser for a large number of plants, moving seeds in larger quantities and distances than any other large African vertebrate (Blake et al., 2009). Through a control of rainforest floristic composition, forest elephant occurrence is associated with increased forest biomass (Malhi et al., 2016) and increased carbon storage capacity (Berzaghi et al., 2019). These processes are thought to drive distinctive structural characteristics in African rainforests compared to their Amazonian and Asian counterparts, with the former exhibiting smaller, but larger tree species, of higher wood density, despite comparable climatic and edaphic conditions (Berzaghi et al., 2019, 2023). African forest elephants hold significant cultural value, contributing to the identity and traditions of Indigenous communities such as the Baka people, for whom ritual and religious practices associated with elephants have historically played a central role (Ngouhouo Poufoun et al., 2016). Nowadays, forest elephants also play an economic role through wildlife tourism.

Due to political and logistical issues constraining survey efforts, the understanding of forest elephant population status is still incomplete, compared to the better-documented savanna elephant (Blake et al., 2009). Nevertheless, the forest elephant has been classified as critically endangered under IUCN Red List criteria A2abd[2], reflecting a severe population decline over the last three generations (IUCN, 2024). Literature highlights a "*devastating decline*" (Maisels et al., 2013) and "*an unprecedented state of conservation crisis*" (Blake et al., 2009). Central African populations have indeed experienced a 62% reduction between 2002 and 2011, now occupying less than 25% of their potential range (Maisels et al., 2013). Recent analysis indicated an approximate 90% decline in forest elephant density at surveyed sites between 1964 and 2016, surpassing the 70% decline observed in savanna elephants over the same period (Edwards et al., 2024). Gabon, which is estimated to support 50% of current Central African population (Laguardia et al., 2021), recorded a 80% decline in a major protected area, the Minkébé National Park, over a ten-year period (Poulsen et al., 2017). In the DRC, historically home to the largest forest elephant populations, the species has been extirpated from over 95%

[2] The IUCN Red List criteria A2abd refers to refers to a ≥30% population decline over the past three generations or 10 years, based on direct observations (a), abundance indices (b), and exploitation data (d), where the causes may not be reversible, understood, or ceased.

of its original range (Maisels et al., 2013), with remaining local populations considered close to extinction (Poulsen et al., 2017). Western African populations are now restricted to a few small and isolated habitat patches (Thouless et al., 2016). These declines are attributed to a combination of factors, including illegal wildlife trade and habitat loss from deforestation, forest degradation, agricultural expansion and logging activities (Thouless et al., 2016). Central Africa has suffered from the highest levels of poaching on the continent, largely driven by the global demand for ivory and bushmeat (Wasser et al., 2015) and exacerbated by human-elephant conflicts, corruption and low enforcement of conservation laws (Breuer et al., 2016). Climate change is anticipated to further amplify drivers of population loss (Nampindo & Randhir, 2024). In this context, protected areas serve as critical refugia for forest elephant conservation, playing a critical role in sustaining remaining populations (Correa et al., 2024).

In West and Central Africa, temperatures are anticipated to rise by 1.5 to 6°C with respect to preindustrial levels by 2100, depending on future greenhouse gas emissions and deforestation scenarios (Abernethy et al., 2016; Akkermans et al., 2014; Haensler et al., 2013). Changes in Central African precipitation patterns are expected but remain subject to uncertainty, due to a scant weather station network and an insufficient understanding of regional radiative forcing (James & Washington, 2013). Regional models exhibit high divergence in both the direction and magnitude of changes (Asefi-Najafabady & Saatchi, 2013; Maidment et al., 2015). In the more deforested West Africa (Crook et al., 2023), similar uncertainty prevails, although observational studies point towards increasing droughts: a long-term drying effect observed over the last decades has been associated with changing forest compositions, including an increase in deciduous, light-demanding species (Aguirre-Gutiérrez et al., 2020; Asefi-Najafabady & Saatchi, 2013; Fauset et al., 2012).

There is emerging evidence of climate change impacts on other elephant species, including *L. africana* in Eastern and Southern Africa and *Elephas maximus* in Asia. Studies employing species distribution models have projected significant range shifts for *L. africana*. For example, at the continental level, unsuitable habitat is projected to increase from 12.7% to 14.1% by 2050, while highly suitable areas are expected to decline from 51.3% to 67.6% under RCP 4.5 and RCP 8.5 (Dejene et al., 2021). Similarly, Mpakairi et al. (2020) estimated a 49% reduction in suitable habitat for *L. africana* in Zimbabwe. In Southeast Asia, *E. maximus* is projected to lose approximately 41.8% of its habitat by 2070 due to the compounding effects of climate change and other anthropogenic threats (Kanagaraj et al., 2019). In Kenya's Amboseli ecosystem, increased rainfall under RCP 2.6, 4.5 and 8.5 has been associated with population growth for savanna elephants (Aduma et al., 2018). However, certain age groups, particularly young calves and older individuals (>40 years), exhibit heightened vulnerability to climate-induced stressors such as droughts, heat waves and disease outbreaks (Foley et al., 2008; Nampindo & Randhir, 2024). Loss of older individuals could have profound implications for herd dynamics such as disruption of matriarchal social structure, migratory patterns and access to water and forage resources. In Botswana, cyanotoxin poisoning driven by a hotter, drier climate has led to mass mortality events, underscoring increasing disease risk (Wang et al., 2021). The risk of foot-and-mouth disease outbreaks, a well-known threat to *L. africana* health, is also expected to change with rising temperature (Jiang et al., 2020).

While the projected impacts of climate change on *L. africana* are the subject of a growing literature, its effects on the forest elephant remain largely unexplored. A notable exception is a long-term study in Lopé National Park, Gabon, which documented an 11% decline in forest elephant body mass between 2008 and 2018, coinciding with an 82% reduction in fruiting events over a 30-year period (1986-2018, Bush et al., 2020b). Although the extent of this phenomenon across the species' range is uncertain, a decline in fruit availability is likely to disrupt energy budgets, exacerbate physiological stress, impair reproductive success and amplify human-elephant conflicts (Blake & Maisels, 2023). Beyond this study, significant knowledge gaps persist regarding how climate change will alter climatic suitability within the species' range, and particularly within protected areas necessary to its persistence.

In this study, we apply a bioclimatic envelope modeling framework[3] coupled with an ensemble forecasting approach to assess projected shifts in the forest elephant's future climatic space. Specifically, we seek to address the following questions: will the forest elephant retain its climatic suitability within their current range by 2100? To what extent will protected areas continue to provide climatically favorable habitats for the species?

Methods

Occurrence data

We conducted all analyses using the R software (R Core Team, 2025). First, we extracted forest elephant occurrence data from two databases: the Global Biodiversity Information Facility

[3] A bioclimatic envelope modeling is a species distribution modeling approach that defines a species' suitable habitat based on climatic variables (e.g., temperature or precipitation) from known occurrence data.

(GBIF; http://www.gbif.org) and iNaturalist (https://www.inaturalist.org). We included records identified as *L. cyclotis* (1,875 records), *L. africana* subspp. *cyclotis* (114 records) and records classified as *L. africana* pre-2021 (when *L. africana* and *L. cyclotis* were not described as two distinct species) and falling within *L. cyclotis* geographic range (944 records). We cleaned occurrence points by removing duplicates (i.e. records with identical geographic coordinates), records lacking geographic coordinates or falling outside the geographic range (using range maps published by the IUCN). This process resulted in 2,933 occurrence records. We delineated our study region by identifying all terrestrial biomes containing at least one forest elephant occurrence record, under the assumption that these biomes represent ecologically accessible habitats for the species. The selected biomes included tropical & sub-tropical moist broadleaf forests, tropical & sub-tropical grasslands, savannas & shrublands and montane grasslands & shrublands within Africa. We applied a spatial thinning process to retain one occurrence per pixel within the study region and produced a final dataset of 293 unique occurrences. Given the large home range of forest elephants (Blake & Maisels, 2023) and the spatial uncertainty inherent in forest elephant survey data (Thouless, 2016), all analyses were conducted using a spatial resolution of 18.5 km × 18.5 km per pixel.

While this dataset (hereafter referred to as Dataset 1) constitutes the only readily available regional dataset of *L. cyclotis* occurrences, it presents bias and data quality limitations, including spatial clustering in the western part of the species' range and low positional accuracy[4]. Moreover, while those occurrences represent remnant populations, they likely do not reflect the breadth of climatic conditions suitable for forest elephants. To address these issues, we generated an alternative dataset (referred to as Dataset 2). Following a protocol developed for the InSiGHTS (Integrated Scenarios of Global Habitat for Terrestrial Species) modeling framework (Visconti et al., 2016), we produced pseudo-presences by sampling the centroids of a 10 arc-min grid intersecting the species geographic range (IUCN, 2025).

Predictor variables

We selected predictor variables following a two-step process: 1) to assess multicollinearity between variables, we performed a variance inflation factor (VIF) analysis, which measures how much the variance of a model is inflated when there is correlation, using the "usdm" package (Naimi, 2012) and setting the VIF threshold at < 6; 2) to ensure that selected predictor

[4]The positional accuracy of retrieved occurrences was low because database users increased the coordinate uncertainty of records to enhance species protection (ranging from 34,000 to 38,248 meters).

variables had ecological relevance for the forest elephants, we conducted a literature review (Beirne et al., 2021; Blake & Maisels, 2023; Breuer et al., 2016; Campos-Arceiz & Blake, 2011; Thouless, 2016) and consulted ecological experts. We first considered 19 bioclimatic variables, encompassing 11 temperature and 8 precipitation-related metrics from the WorldClim database (Hijmans et al., 2005), frequently utilized to produce species distribution forecasts under climate change (Guisan et al., 2017). Generally, temperature variables define thresholds beyond which mammalian metabolism and reproduction may be compromised (Mitchell et al., 2018), while precipitation reflects water availability, vital for survival, and both serving as indirect proxies for plant abundance (Gillman et al., 2015, cited by Biancolini et al., 2024). After the selection process, we retained the following variables: maximum temperature of the warmest month (bio5), minimum temperature of the coldest month (bio6), precipitation seasonality (bio15), precipitation of wettest quarter (bio16) and precipitation of driest quarter (bio17, Supplementary material). We projected all spatial data into the WGS84 Mercator coordinate system. We considered five Global Circulation Models (IPSL-CM6A-LR, MIROC6, MPI-ESM1-2-HR, MRIESM2-0, UKESM 1-0-LL, Eyring et al., 2016), and selected two emission scenarios: SSP 245, representing an intermediate greenhouse gas emission trajectory, and SSP 585, a high-emission pathway. We excluded SSP 126, a low-emission scenario, due to its decreasing relevance under current global greenhouse gas emission trends. For current conditions, we used bioclimatic variables averaged over the 1950-2000 period, while future climate projections were based on time periods centered around 2100 (Hijmans et al., 2005).

Species distribution model and ensemble forecasting

For Dataset 1, we applied a target-group background approach, which is considered a key strategy to address sampling bias in species occurrence records. This method leverages the combined occurrence data of ecologically similar taxa within the same region to approximate sampling effort for the focal species (Barber et al., 2022). The underlying assumption is that surveyors exhibit comparable biases when recording taxa with shared traits, thereby enabling a broader dataset to reflect general sampling intensity. Specifically, we used the COMBINE dataset (Soria et al., 2021) and included all African megafaunal species, defined as those with an adult body mass exceeding 40 kg (Malhi et al., 2016). We obtained a dataset of 537 species and extracted all occurrence records from GBIF and iNaturalist (124,422 records). After applying a thinning process similar as the one implemented for Dataset 1 occurrences, we obtained 13,378 target-group occurrence points. For the Dataset 2, following the InSiGHTS framework, we generated 10,000 pseudo-absences by randomly sampling along a 10 arc-min grid, outside the forest elephant range, and within the study area.

In order to model the distribution of the forest elephant, we employed an ensemble forecasting approach, i.e., an approach combining predictions from multiple individual models to control for the effect of model type uncertainty (Araújo & New, 2007; Valavi et al., 2021). Using the "sdm" package (Naimi & Araújo, 2016), we integrated three modeling algorithms: generalized additive model (GAM), maximum entropy modeling (MaxEnt) and boosted regression trees (BRT). GAM is an extension of generalized linear models that uses nonparametric smooth functions to capture nonlinear relationships between response and predictor variables. MaxEnt, a widely used presence-only algorithm, estimates the probability distribution of a species by maximizing entropy while constraining it to match known occurrences. BRT is a machine-learning method that sequentially fits an ensemble of regression trees in a forward stagewise fashion, minimizing residual error (Thuiller et al., 2009). We retained default settings for all algorithms.

To evaluate the predictive ability of the models, occurrence and background datapoints were randomly split into a training (80% of datapoints) and a testing (20%) datasets, and this process was reiterated five times. We used two complementary metrics: the Area Under The Curve (AUC) and the True Skill Statistic (TSS). AUC (ranging from 0 to 1) measures a model's ability to distinguish presence from absence locations, while TSS (ranging from -1 to 1) evaluates classification accuracy by accounting for both false positives and false negatives. Together, these metrics provide a holistic evaluation of predictive performance in species distribution models (Sillero et al., 2021). Following established standards, we retained models with AUC values > 0.7 and TSS values > 0.6.

We then combined these models using an average method to produce the final probabilistic predictions (Araújo & New, 2007). In order to facilitate cross-datasets comparison, we generated binary suitability maps. We applied a threshold corresponding to the 10^{th} percentile of model predictions (Jung, 2023), summing the binarized climate model to obtain values from 0 to 5 and classifying pixels as suitable if at least 3 out of 5 models indicated presence. To test the sensitivity of the results to the chosen threshold, we also generated binary maps using a 5% and 15% threshold (Supplementary material). Given the current conservation status of the forest elephant, and the highly fragmented nature of its habitat, we adopted a conservative view of future distribution under climate change, and assumed no dispersal beyond its current range, following Pacifici et al. (2020). We identified areas of sustained climatic suitability in the future, as well as areas of climatic suitability loss, i.e. currently suitable regions that are projected to become unsuitable under future climate change scenarios. We generated consensus maps highlighting regions of model agreement across datasets (Dataset 1 and 2) and across climate scenarios (SSP 245 and SSP 585), identifying areas of habitat loss (pixel unsuitable based on both datasets) or habitat gain (pixel suitable based on both datasets). Areas of consistent suitability across both datasets and scenarios were designated as climatic refugia for forest elephants. To assess conservations implications, we overlapped the consensus maps with protected area coverage and with projected forest cover loss by 2100 (Vieilledent et al., 2023).

Results

Model performance and relative variable importance

Overall, our models exhibited high predictive ability, with Dataset 1 models presenting AUC values ranging from 0.878 to 0.935 (mean value = 0.9235, within the excellent range of performance), and TSS values from 0.6220 to 0.8005 (mean value = 0.7312, considered “good”). For Dataset 2 models, AUC values ranged from 0.950 to 0.960 (mean value = 0.9558, in the excellent range) and TSS values from 0.7728 to 0.8069 (mean value = 0.7995, “good”, Supplementary material).

In the first model (Dataset 1), the most important bioclimatic variables predicted for the forest elephant was the minimum temperature of the coldest month (bio6), followed by precipitation of the wettest quarter (bio16), maximum temperature of the warmest month (bio5), precipitation seasonality (bio15) and precipitation of driest quarter (bio17). In the second model (Dataset 2), precipitation seasonality (bio15) came first, followed by precipitation of the wettest quarter (bio16), minimum temperature of the coldest month (bio6), precipitation of driest quarter (bio17) and maximum temperature of the warmest month (bio5, Supplementary material).

A contraction in future *L. cyclotis* climatic space

Our findings (Figure 1) indicate a contraction in climatically suitable habitat under both datasets, with a more pronounced decline in Dataset 1 (by 32.43 and 36.14% under SSP 245 and SSP 585, respectively) compared to Dataset 2, which projects a slight increase (+1.12%) under SSP 245 or a moderate decline (-7.67%) under SSP 585 by 2100. Under Dataset 1, projections indicate a significant contraction of climatically suitable areas in the central Congo Basin, accompanied by increasing fragmentation in West Africa, despite the emergence of small, isolated patches (Figure 1). Under SSP 585, core suitable areas in the western Congo Basin experience substantial losses. Projections derived from Dataset 2 suggest more moderate shifts in climatically suitable conditions. While core areas within the Congo Basin appear to exhibit relatively stability, projections under SSP 585 nevertheless indicate a declining suitability in central areas, as well as a peripheral shrinkage, particularly along the northwestern and southern margins.

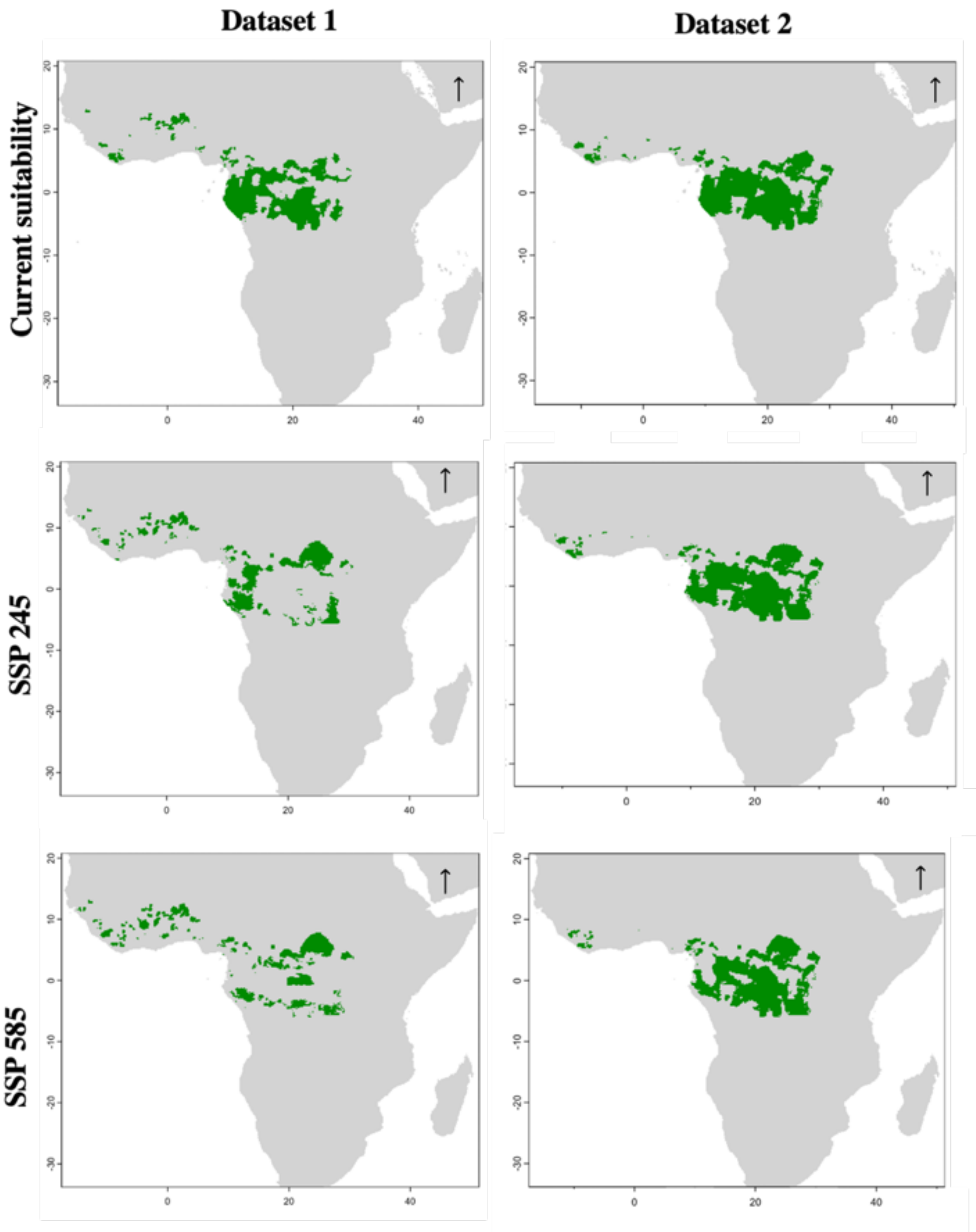

Figure 1: Ensemble binarized current and forecast climatic suitability within the range of the forest elephant (forecast based on SSP 245 and SSP 585 scenarios). The two columns represent the two occurrence datasets (Dataset 1 and Dataset 2).

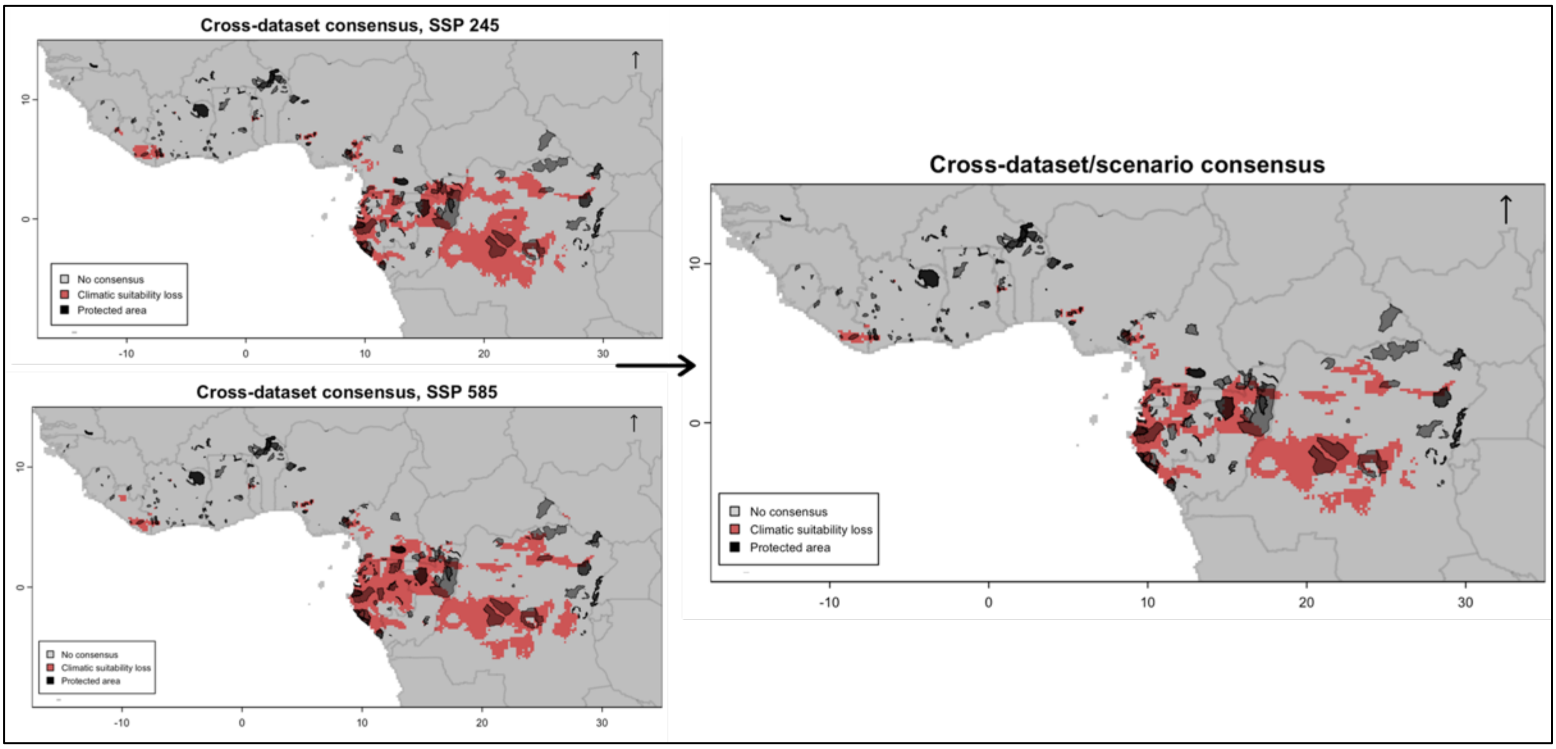

Figure 2: In red, consensus projections of climatic suitability loss across Dataset 1 and Dataset 2 (left) and consensus projections across Dataset 1 and Dataset 2, and SSP 245 and SSP 585 (right), overlayed with current protected area coverage, in black. Data source: World Database on Protected Areas.

Spatial agreement across Dataset 1 and 2 and SSP scenarios delineates consensus regions of projected climatic suitability loss, predominantly concentrated in the central DRC, northern Republic of Congo and parts of Gabon (Figure 2). Notably, while most of Gabon retains climatic suitability across datasets under SSP 245, this suitability diminishes substantially under SSP 585. When considering consensus across datasets and scenarios, approximately 46.04% of the current protected area coverage is projected to lose climatic suitability.

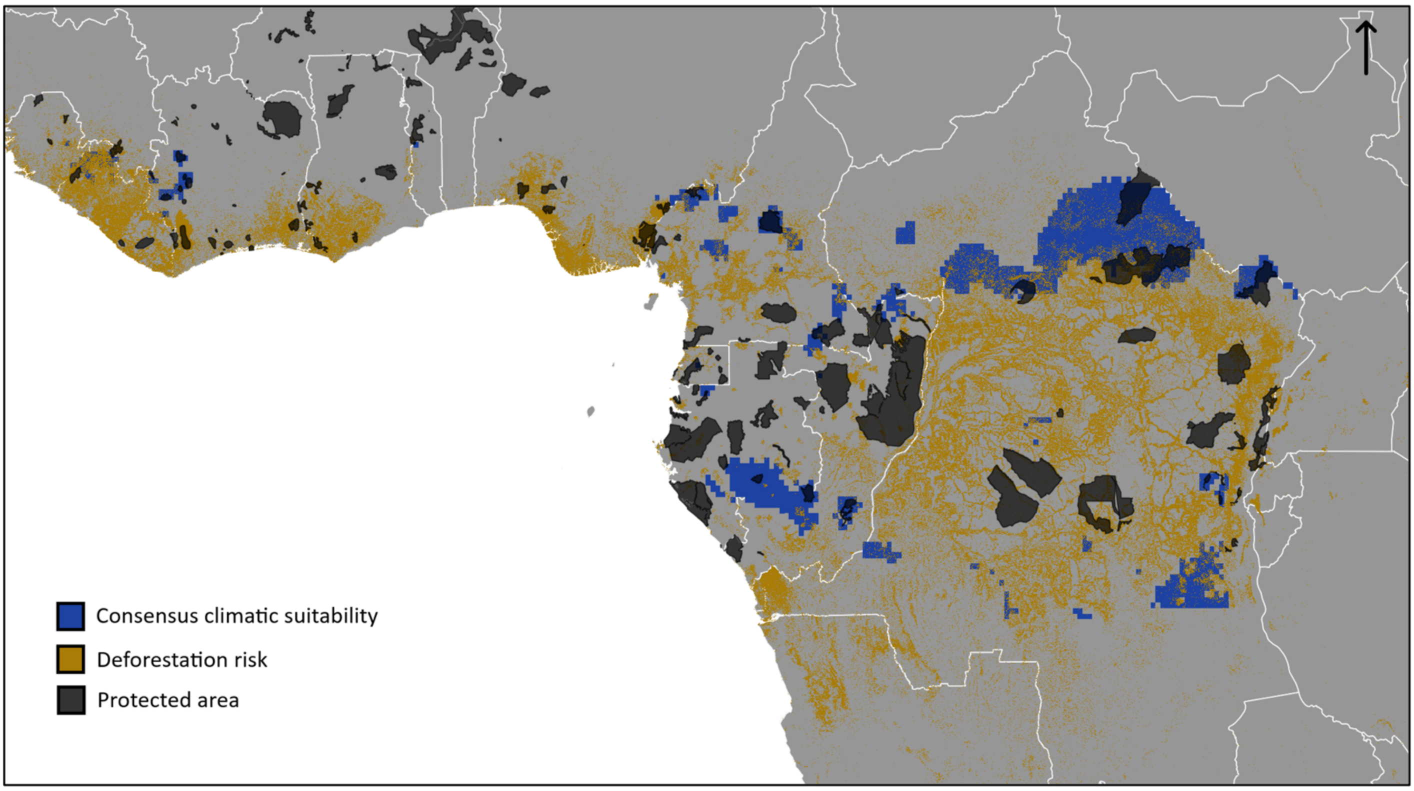

Figure 3: Consensus projection of climatic suitability for forest elephants across Dataset 1 and 2 and SSP 245 and SSP 585, in blue, overlaid with deforestation risk by 2100. Data source: Vielledent et al., 2023.

Spatial agreement across Dataset 1 and 2 and SSP scenarios indicates the occurrence of climatic refugia in the northern extent of the forest elephant range, particularly in the southern Central African Republic and along the southwestern and northeastern periphery of the species range (Figure 3). These regions may serve as critical strongholds for the species under projected climate conditions. However, habitat stability is further threatened by deforestation risk. Under a business-as-usual deforestation trajectory for the 21st century, the central Congo Basin (particularly the DRC) is projected to experience pronounced forest fragmentation, leading to an increasing number of smaller patches, isolated from a comparatively intact rainforest block in the western Congo Basin (Vieilledent et al., 2023). Notably, we observe an overlap between projected areas of climatic suitability, consistently identified across datasets and scenarios, and regions of high deforestation risk, particularly in the northern Congo Basin (Figure 3). Approximately 12.85% of consensus regions expected to maintain favorable climatic conditions are projected to coincide with areas experiencing high deforestation risk by 2100.

Discussion

In this study, we used an ensemble bioclimatic envelope modeling approach to predict future climatic suitability for the forest elephants under two emission scenarios (SSP 245 and SSP 585, Eyring et al., 2016). We present here findings derived from two alternative datasets, each capturing opposing extremes in data representation: one presenting actual, but geographically biased occurrences and another employing a hypothetical distribution, assuming forest elephant presence across its entire range. Our results reveal a consistent cross-dataset and cross-scenario signal of climatic suitability loss, moderate under SSP 245 and more pronounced under SSP 585. Notably, the loss of climatic suitability is projected to occur in key conservation areas, including protected areas located in the western and central parts of the forest elephant range. When integrating future deforestation risk - particularly in the central Congo Basin, with the highest rates observed in the DRC - the projected habitat outlook deteriorates further. As obligate forest dwellers, forest elephants may face synergistic anthropogenic and climatic threats that could significantly reduce their likelihood of long-term persistence. The compounding effects of climate change and existing anthropogenic pressures require urgent consideration from a conservation perspective, as discussed below.

Bioclimatic envelope modeling and data limitation

Modeling species' responses to global environmental change inherently involves uncertainties (Araújo & New, 2007; Thuiller et al., 2019). We addressed some of these by implementing an ensemble modeling framework, accounting for variability across climate models and climate scenarios and focusing on a limited number of critical predictors. However, incomplete sampling of the species' range remains a significant limitation - particularly in Western and Central Africa where indirect survey methods (e.g. road transects, dung counts and trail surveys) prevail (Thouless, 2016). This is compounded by the logistical difficulties inherent in sampling vast, remote areas (De Boer et al., 2013), as by the scarcity of historical data and the pronounced human-driven contractions of the species' current distribution (Martínez-Freiría et al., 2016), potentially narrowing the breadth of climatic conditions assessed in projections under Dataset 1. To mitigate this potential bias and obtain a more comprehensive assessment of potential future climatic suitability, we compared estimates using Dataset 2. Despite these limitations, ensemble correlative models remain effective tools for assessing climate change impacts and informing conservation strategies under uncertainty.

Implications for forest elephant conservation

The illegal wildlife trade coupled with advancing deforestation is driving a precipitous decline in forest elephants across much of their range, resulting in extensive expanses of forest void of their presence (Blake & Maisels, 2023). Given the severity of threats facing forest elephant populations, accurately predicting future climatic suitability within their range is essential for informing conservation strategies and ensuring their long-term survival. Protected areas, which currently constitute 14.9% of land-use in Central Africa (Eba'a Atyi et al., 2022), are increasingly becoming critical refuges for megaherbivore populations. However, our projections reveal a 46.04% contraction of the climatic space available to forest elephants within the existing protected area network.

Considering the Target 3 of the Kunming-Montreal Global Biodiversity Framework, which aims to protect at least 30% of terrestrial and inland water areas by 2030 (CBD, 2022), and with the view to mitigate deforestation risks, forest elephant range countries should prioritize regions projected to maintain future climatic suitability for the designation of new protected areas, particularly in the northeastern extent of the species' range. In the western part of the forest elephant range, ensuring long-term access to refugia habitats, by integrating adaptive management strategies enhancing connectivity, should be considered a key priority in conservation planning under climate change (Deb et al., 2019).

Despite the steep decline in forest elephants across their range, relatively stable forest elephant populations persist in Gabon and the northern Republic of Congo (Laguardia et al., 2021). The conservation of those population strongholds is paramount. Our findings indicate that climatically suitable conditions appear to persist in both those countries, but their extent is predicted to diminish substantially under a SSP 585 scenario. Given this anticipated reduction in climatic suitability, mitigating non-climatic threats to forest elephants within these regions becomes imperative to ensuring their long-term survival.

A key challenge in this context is the escalating incidence of human-elephant conflicts, which are already a significant management challenge in Gabon due to high elephant densities (Guarnieri et al., 2024). Climate change further accentuates these challenges by threatening rural livelihoods, triggering shifts in human population density and agricultural expansion. Additionally, a climate change driven-decline in food availability, as reported by Bush et al. (2020b) in the Lopé National Park, Gabon, could play an exacerbating role, by driving forest elephants into agricultural fields in the search of alternative food resources. With increasing climate change and a reduced climatic space for the forest elephants (especially under SSP 585), human-elephant conflicts are expected to rise in severity, as is projected for both *E. maximus* and *L. africana* (Guarnieri et al., 2024). Failure to implement such integrative strategies may further undermine the long-term persistence of forest elephants within their remaining climatic refugia.

Given the projected contraction of climatically suitable space within protected areas, specifically in the western and central part of the forest elephant range, it is crucial to explore alternative conservation strategies beyond traditional protected areas. In Central Africa, logging concessions account for approximately 32.3% of land-cover (Réjou-Méchain et al., 2021), presenting opportunities for integrated conservation approaches. When managed effectively, these concessions can contribute to forest cover preservation, maintain essential ecological functions while serving as biodiversity corridors and facilitating connectivity between protected areas and climate refugia, provided that robust legislative and certification standards are met (Réjou-Méchain et al., 2021). For example, Munshi-South et al. (2008) documented forest elephant occurrence within a protected area-infrastructure mosaic in the Gamba complex in Gabon, noting their adaptation to oil extraction sites following the implementation of stress-reduction measures. Similar integrative approaches, illustrated by mixed-use landscape designs to promote elephant dispersal, are already investigated in other contexts, including Sumatra (Imron et al., 2023).

Other relevant climate change impacts on *L. cyclotis*

Other relevant impacts of climate change on forest elephants should be taken into consideration in a conservation planning context. While research has documented the vulnerability of *L. africana* to excessive heat due to their limited phenotypic adaptation for thermoregulation - particularly when ambient temperature exceed 40°C (Mpakairi et al., 2020) - similar physiological constraints are relevant for forest elephants despite their distinct ecological niche. The increasing frequency and intensity of extreme temperature events may therefore also constitute a substantial physiological burden for the forest elephants (Beirne et al., 2020). Forest elephants employ thermoregulatory mechanisms akin to those observed in their savanna counterparts, including high reliance on water, and hence require substantial water intake (Dejene et al., 2021). In both the Republic of Congo and Gabon, empirical studies corroborate the role of water availability as a primary determinant of elephant distribution and movement patterns (Beirne et al., 2021; Blake & Maisels, 2023). Forest elephants are hypothesized to exhibit bimodal ranging behavior, with dry season movements constrained around perennial water sources such as rivers and swamps, whereas wet season movements are influenced by fruiting tree distribution (Beirne et al., 2021). During periods of water scarcity, elephants preferentially remain in proximity to stable water sources. Despite the high annual rainfall characteristic of Central African tropical forests, forest elephants may still experience water limitations under increasing climate change. These considerations are essential for conservation planning, particularly in the design of biodiversity corridors that connect climate refugia, ensuring access to critical water resources and reducing potential physiological stressors associated with climate change.

Our models indicate that the minimum temperature of the coldest month (bio6) and precipitation of the wettest quarter (bio16) are the primary bioclimatic predictors of forest elephant presence, both of which are closely linked to foraging disruptions. The critical minimum temperature hypothesis posits that flowering in certain Afrotropical plant species is initiated only when ambient temperatures fall below a certain threshold (Tutin & Fernandez, 1993). As global temperatures increase, the frequency of thermal cues is expected to decline, potentially reducing the incidence of reproductive events in fruiting trees. Similarly, future increase in temperature and shift in precipitation are anticipated to negatively impact forage availability by intensifying extreme weather events - such as droughts and frequent fires (Bush et al., 2020b; Dejene et al., 2021) - thereby reducing the fructification of elephant-dispersed species. For example, *Sacoglottis gabonensis*, an influential species in elephant movement and seed dispersal (White, 1994), exhibits rainfall-dependent fruiting patterns, suggesting that changes in precipitation could affect its fruit production. Similarly, *Sarcophrynium prionogonium* shows reduced growth, fruiting and dispersal capacity under increasing aridity, while *Angylocalix oligophyllus* is projected to experience a contraction in its distributional range under future climate scenarios (Beekmann et al., 2024). Although our framework does not explicitly model these ecological processes, they are partially reflected in the response of bio6 and bio16. Ultimately, a projected decline in food quality and availability, driven by climate and land-use changes, may emerge as a critical limiting factor for forest elephants (Bush et al., 2020b).

Lastly, the forest elephant exhibits life-history traits which could contribute to its vulnerability under climate change (Advani, 2014). Although the species demonstrate high dispersal capacity, its efficacy is undermined by increasing habitat fragmentation in West and Central Africa. With a generation time of approximately 25 years, a 22-month gestation period and inter-calving intervals of 4 to 6 years, forest elephants display low reproductive and population growth rates, which constrain its capacity for population recovery (Turkalo et al., 2017).

Furthermore, reproduction is tightly coupled with rainfall dynamics. Birth peaks coincide with periods of high rainfall, while drought conditions, adversely affecting vegetation productivity, impair the nutritional status and breeding readiness of females.
The forest elephants are a species of global conservation concern, having experienced a dramatic population decline over the past century and now persisting in increasingly fragmented and isolated populations. Climate change is projected to further exacerbate the species' vulnerability and undermine its long-term viability (Nampindo & Randhir, 2024). The decline of forest elephants could have profound ecological repercussions for Congo Basin ecosystems, as their role as keystone megaherbivores is essential for maintaining forest structure, facilitating seed dispersal and potentially enhancing the resilience of Congo Basin rainforests in response to climate change. Consequently, our findings underscore the urgent need to integrate climate change-related considerations into conservation planning to ensure the persistence of forest elephants, crucial stewards guardians of Congo Basin rainforests, throughout the 21st century.

Forest elephant in the morning mist. Photo by J.V., site manager of the Mbeli Bai site, Nouabalé-Ndoki National Park, during my visit in December 2023.

Chapter V
General discussion

Key findings and relevance of results

In the concluding section of the introduction, I outlined the primary objectives of the analytical chapters presented in this thesis (Chapters II to IV). This section provides a concise synthesis of key findings, emphasizing their contributions to both the overarching framework of the thesis and the broader literature.

Chapter II: Uncertain future for Congo Basin biodiversity: A systematic review of climate change impacts

This chapter presented a systematic review of the literature linked with current and projected climate change impacts on biodiversity in the Congo Basin. My findings indicated that all organizational levels of biodiversity, from genes to ecosystems, are either already impacted or projected to be affected by climate change in the future. However, this review revealed critical gaps in the literature, fueled by a substantial disparity in scientific effort between the Congo Basin and the Amazon Basin, and resulting in limited empirical evidence of climate change-driven ecological responses. Entire taxonomic groups, including freshwater organisms, amphibians or reptiles, remain largely overlooked. Key ecological processes studied in other regions, such as climate change-driven evolutionary adaptation or shifts in trophic interactions (Scheffers et al., 2016), are also poorly documented. Importantly, climate change is projected to interact with other drivers of change, including deforestation and forest degradation (Yuh et al., 2024), but the manifestation of this nexus in the region is unexplored, which constitutes a major research priority.

In this chapter, I established the foundation for my thesis, identifying critical knowledge gaps to address in subsequent investigations, explored through field-based research in Chapter III and species-specific modeling in Chapter IV. Beyond its role in guiding my doctoral research, this chapter also contributes to the broader field of climate change and biodiversity research in an important tropical region. By systematically classifying climate change impacts across all biodiversity organizational levels, it proposes a methodological approach for replication in future studies, particularly in other biodiversity hotspots. Through a consolidation of fragmented research efforts, the findings strengthen the foundation for future interdisciplinary collaboration among climatologists, ecologists and conservation biologists, essential for anticipating biodiversity loss in the Congo Basin.

Chapter III: "We saw fish in the cocoa farm": Local observations of the impacts of climate change on biodiversity and livelihoods in the Lac Télé Community Reserve, Congo Basin

This chapter examined the local-scale impacts of climate change on biodiversity and human livelihoods in the Lac Télé Community Reserve, Republic of Congo, leveraging both local ecological knowledge and meteorological data. Instrumental data indicated a warming trend of 0.39°C per decade (± 0.007 SE) in 1990-2023, and a moderate increase in long dry season rainfall (+26.4 mm per decade, ± 0.46 SE). This contrasts with regional satellite estimates, which reported an annual mean temperature increase of 0.15°C per decade (Collins, 2011) and with drying trends observed in several other Congo Basin sites (Bush, et al., 2020a). Local ecological knowledge further revealed wide-ranging biodiversity impacts, including increased tree mortality, altered fish reproduction and disrupted mammal migration patterns. This chapter also identified over 30 local adaptation strategies spanning various aspects of subsistence and habitations, all of which are household-driven, rather than initiated by institutional or non-governmental stakeholders.

This represents the first study to investigate the effects of climate change on biodiversity within the Lac Télé Community Reserve, providing important socio-ecological baseline documentation of this understudied site, and is among few studies to examine this question in a Congo Basin swamp forest ecosystem. Findings are supported by a notably large dataset for research of this kind, comprising 191 interviews (structured and non-structured) and 8 focus group discussion. Conducted within the LICCI (Local Indicators of Climate Change) framework, this research refined methodologies for assessing biodiversity impacts through local ecological knowledge. Climate change impacts observed by Reserve inhabitants may reflect broader regional patterns in other floodplain ecosystems, highlighting the need to assess shifts in seasonal flooding and rainfall across swamp forests, seasonally inundated sites and other habitat types. If the impacts - including decline in fruit availability - reported by respondents are widespread across the Reserve and the broader Congo Basin, it could have profound ecological ramifications, notably for *Gorilla gorilla gorilla*, a key frugivorous species

(Masi et al., 2009, 2015). Finally, given the scarcity of climate change adaptation research in Central Africa, this study also provides one of the first identification of indirect climate change impacts on biodiversity in the Congo Basin.

Findings suggest that local ecological knowledge of floodplain dynamics remains highly developed within the Reserve, particularly regarding its complex hydrological system and influence on climatic and ecological patterns. With 90% of floodplain ecosystems lost in the Northern Hemisphere (Crook et al., 2020), the Reserve represents an important site where local knowledge of flood pulse dynamics persists. While remote sensing has been the primarily instrument for compensating the lack of ground-based research in the Congo Basin, this study demonstrates that local ecological knowledge provides an essential complementary approach, enabling a rapid, cross-taxon assessment of ecological changes.

This chapter is supplemented by an ethnographic study entitled "*Fine-scale human-flood relationships in the Congo Basin: Ethnographic perspectives from the Lac Télé Community Reserve*", which investigates village-specific and catchment-wide mechanisms by which local communities observe, interpret and respond to dynamic hydrological processes within the Reserve (Supplementary material).

Chapter IV: Shrinking climatic space: Implications for forest elephant conservation in the Congo Basin under climate change

In this chapter, I performed a regional-scale analysis assessing future climatic suitability in *L. cyclotis* range under climate change, employing a bioclimatic envelope modeling and an ensemble forecasting approach under a low emission (SSP 245) and a high emission (SSP 585) scenarios. Findings revealed a cross-model, cross-scenario signal for climatic suitability loss in the Central Congo Basin. Critically, projections suggested that about half of current protected area coverage will lose climatic suitability by 2100. Remaining areas with projected climatic suitability are also projected to overlap with areas of deforestation risk. Considering the species' keystone role in structuring Congo Basin rainforests (Asefi-Najafabady & Saatchi, 2013), the conservation of remaining forest elephant population is of particular importance for maintaining rainforest resilience under global and climate changes.

The lack of long-term monitoring of forest elephants, particularly the absence of high-resolution occurrence records with low positional accuracy, posed a significant challenge for this analysis. We considered available datasets derived from GBIF and iNaturalist to be somewhat unreliable due to sampling biases, which could introduce uncertainty in bioclimatic envelope model projections. To mitigate these limitations, this chapter introduced a methodological innovation (to our knowledge), by developing a two-dataset approach. First, I used existing occurrence data, acknowledging its inherent biases. Second, I artificially reconstructed a more comprehensive occurrence dataset, reflecting the full known extent of *L. cyclotis* based on expert assessments. By identifying areas of agreement between the two models, I generated a more robust estimate of future climatic suitability.

Limitations and future research

As highlighted in Chapter II, significant knowledge gaps remain in understanding the interactions between climate change, biodiversity, human adaptations and the indirect impacts of climate change on Congo Basin ecosystems. While this thesis addresses key aspects of these dynamics in Chapters III to IV, it does not comprehensively assess all the facets of these complex relationships. Some of the limitations are discussed below.

As noted in Chapter II, the lack of long-term field monitoring in many Congo Basin sites severely constrains our understanding of ongoing climate change impacts. Many studies rely on remote sensing or modeling, leading to uncertainties in projected biodiversity changes. Expanding on-the-ground ecological research and monitoring programs is essential for proper ground-truthing. Furthermore, my analysis was limited to peer-reviewed literature published in English, with gray literature in both English and French incorporated to mitigate knowledge gaps. Additional relevant information - including unpublished documentation or reports that are not unavailable online - likely exists at the local level. An expert-driven literature identification process, targeting unpublished data, historical records and local reports, could serve as a valuable extension of this work. While beyond the scope of this study, such an approach should prioritize academic and local institutions within Congo Basin countries and include French, a widespread language in the region.

Similarly to conventional ecological monitoring methods, data collected through local ecological knowledge approaches are susceptible to biases, which should be accounted for (Brittain et al., 2020). In Chapter III, respondents to our study might have been influenced by factors such as the recency effect and the shifting standard syndrome - a gradual alteration in accepted environmental norms due to diminished knowledge of past conditions (see Fernández-Llamazares et al., 2015; Papworth et al., 2009). Additionally, historical and current factors such as colonization and the environmental crises can exert a compromising influence on IP&LC knowledge systems (Reyes-García et al., 2024a). In the Reserve, the increasing climate unpredictability was cited as a factor affecting the knowledge basis from which respondents form their observations. To enhance data reliability, we implemented robust validation measures, including a large sample size, increased population representativity, mixed-method data triangulation, respondent validation and iterative feedback processes, ensuring that final themes accurately reflected the phenomena under investigation (Golafshani, 2003). Moreover, assessing adaptation measures adopted by Reserve inhabitants proved a complex act, which required frustrating yet sometimes necessary simplifications to effectively interpret and communicate findings. I observed that the drivers of adaptation measures within the complex socio-ecological dynamics of the Lac Télé Community Reserve are rarely independent of one another. While climate change significantly impacts local populations, it was seldom identified as the primary motivator for adaptation. Instead, adaptation strategies such as intensified fishing and agricultural expansion were also shaped by pre-existing socio-economic and environmental stressors, with climate change acting as an aggravating rather than a singular factor. Decision-making was further constrained by considerations such as land tenure norms, conservation regulations and economic barriers (e.g. in the acquisition of new fishing material), limiting options such as agricultural expansion into non-flooded forested areas. A finer-scale analysis of adaptation enablers and constraints is needed to better understand livelihood transitions under global changes in the Congo Basin. Finally, while Chapter III provides an initial identification of the indirect impacts of climate change on biodiversity associated with adaptation measures, quantifying them was beyond the scope of the study. Future research should employ spatially explicit, quantitative analyses to establish causal links between adaptation measures and ecological changes, both within the Lac Télé Community Reserve and across other swamp forest ecosystems.

In Chapter IV, the data limitations presented in previous sections prevented a comprehensive analysis of future *L. cyclotis* distribution under global changes. Future research should seek to integrate other key ecological and anthropogenic variables of relevance for forest elephant ecology, such as distance to water, topography, land cover, human settlement and road proximity.

Considerations and challenges associated with the implementations of decolonial research practices

As a Western researcher affiliated with European academic institutions, I considered the integration of decolonial research principles into the design and execution of this study (and notably its fieldwork component) to be an imperative (Trisos et al., 2021). Such principles are important to ensure the representation of Congo Basin perspectives (Nsah, 2023) and to mitigate the risks of parachute science - wherein researchers from the Global North conduct studies in

Global South countries without substantive engagement, collaboration or acknowledgement of local governance structure, expertise and research capacity structures (de Vos & Schwartz, 2022). Specifically, I took the following measures:

- Prior to starting fieldwork, I conducted discussions on research design, methods and questionnaire development with Congolese scholars (Professors Ifo Suspens Averti and Triomphe Ibiassi) and local experts, including the Lac Télé Community Reserve local WCS team (Bola Madzoké, Roger Mobongo and Gérard Bondeko) and community leaders (Didier Orphas and Rodrigue Moloumba);
- I interpreted results collaboratively through consultations with local stakeholders to ensure contextual relevance;
- I translated results in French and Lingala and facilitated research availability for local institutions and research participants;
- I prioritized Central African scholarly work and bibliographic references, including gray literature and French-language sources, to amplify regional perspectives.

A critical improvement for future work would be to actively co-design research questions with local stakeholders. Prior to fieldwork, I sought input from regional and village-level authorities to ensure that planned research questions aligned with local needs. Given the scarcity of existing studies in the region, the research was generally perceived as valuable. However, developing scientific inquiries with direct local applicability - beyond a post-hoc approach - necessitates prolonged engagement, a deep familiarity with the socio-ecological system under study, local governance structures and power dynamics, as well as the ability to conduct multiple field missions to foster long-term research relationships. The 4-6-week timeframe per village was insufficient for substantive participatory research co-design. Moreover, the institutional constraints of a doctoral research - where resources such as time and funding are constrained - posed structural challenges, particularly in study design and fieldwork execution.

Scientific and policy contributions

Key contributions to climate change and biodiversity research in the Congo Basin

This PhD research makes several key theoretical contributions to the climate-biodiversity scholarship in the Congo Basin. First, it presents a systematic, basin-wide assessment of climate change impacts on biodiversity, synthesizing the current state of knowledge and identifying key gaps in existing research. This synthesis offers a foundational framework for future studies seeking to understand ecosystem shifts in tropical forest systems. Second, this thesis contributes novel empirical data from an underserved floodplain site in the Congo Basin, documenting both direct and indirect climate impacts on biodiversity. These include underreported processes such as altered migratory patterns in several mammal, bird and fish species; increased mortality in tree species; reduced wild fruits production; and emerging adaptation strategies that may represent an additional risk for biodiversity conservation. Third, the study offers original insights into the climate adaptation challenges faced by local human populations, highlighting structural vulnerabilities. This study contributes to a limited body of literature documenting fine-scale human-environment interactions and the role of local ecological knowledge systems in shaping both historic and contemporary adaptation practices. Finally, it includes spatially explicit modeling to project future climatic suitability for a keystone megafaunal species, the forest elephant, whose ecological role is central to Congo Basin rainforest structure and resilience. Using multiple data sources of species occurrence, the analysis reveals potential shifts in the species' climatic niche under projected scenarios, with important implications for conservation strategy and protected area prioritization. Collectively, these contributions offer a robust empirical basis for understanding biodiversity responses to climate change in the Congo Basin and inform adaptive conservation planning at both local and regional scales.

At the methodological level, this PhD research offers two primary contributions to Congo Basin research, via an interdisciplinary and cross-scalar perspective. First, it advances the case for methodological pluralism by bridging local-scale ecological observations with regional-scale assessments. In the face of high environmental variability and pervasive uncertainty, interdisciplinary approaches - spanning ecology, climatology, ethnoecology and conservation science - offer a more holistic understanding of socio-ecological transformations. This research demonstrates that such integrative frameworks are not only methodologically robust, but also essential for capturing the multifaceted nature of climate change-driven ecological change.

Second, it underlines the central role of local ecological knowledge in conservation science in a Congo Basin context. Although local ecological knowledge has been examined in research fields such as ethnoecology or environmental anthropology, its scientific potential remains underutilized within tropical ecology and biodiversity science. While local ecological knowledge has an array of applications in socio-ecological frameworks (e.g. in natural resource governance or the preservation of biocultural diversity), this study specifically emphasizes its value in addressing research questions that would remain inaccessible through conventional scientific methods, particularly in regions with limited ecological monitoring. Local ecological knowledge can serve as an informal early warning system for detecting ecological disruptions and supports context-specific ecological change assessments. By integrating local ecological knowledge with ecological modeling approaches, this study contributes to a scalable framework for multi-source methodologies, offering a pathway toward more inclusive, adaptive and effective conservation science in the Congo Basin.

By identifying research priorities and starting to address key knowledge gaps, a primary objective of this PhD research was to contribute to a revitalized Congo Basin research, establishing a methodological foundation for advancing ecological forecasting, climate change impact assessment and adaptation planning in one of the most under-studied yet ecologically significant regions of the world. The findings open new perspectives on the complex interactions between climate change, biodiversity and human adaptation at multiple scales, and are intended to catalyze further interdisciplinary research to build on and extend this approach.

Policy implications

From a policy perspective, this research underscores the Congo Basin's critical role in global biodiversity conservation, carbon storage and climate change mitigation. Findings presented across this PhD thesis hold implications for policy decision-making at multiple governance scales. At the global level, they contribute to the objectives of the Paris Agreement (UNFCCC, 2015), the Kunming-Montreal Global Biodiversity Framework (CBD, 2022) and the United Nations 2030 Agenda for Sustainable Development (UNGA, 2016). At the regional level, they align with commitments under the Yaoundé Declaration (COMIFAC, 1999), which emphasizes the protection of Congo Basin ecosystems as integral to sustainable development and underscores the necessity for collaborative efforts among member states to promote the sustainable use and conservation of forest resources.

Drawing upon the findings presented across chapters, this research identifies four key policy implications that could support the implementation of these international and regional frameworks, and provides actionable insights for protected area planning, climate resilience strategies and biodiversity policy frameworks in the Congo Basin:

1. <u>Elevating the Congo Basin biodiversity as a priority area in global and regional policy instruments</u>:

While initiatives such as CARPE (the Central Africa Regional Program for the Environment, CARPE, 2025) have supported Congo Basin rainforest conservation efforts, funding remains disproportionately low compared to other tropical forest regions such as the Amazon. Addressing this imbalance requires dedicated funding mechanisms that prioritize research, conservation and sustainable development in the Congo Basin. This thesis' identification of critical research gaps - such as the underrepresentation of certain taxonomic groups and ecological processes - can help direct resources toward the most pressing needs. Emerging efforts inspired by successful initiatives such as the Science Panel for the Amazon, including the Congo Basin Science Initiative (CBSI, 2025) or the Science Panel for the Congo Basin (SPCB, 2025), represent an important step in this direction.

2. Strengthening the integration of local ecological knowledge into conservation policies:

In data-deficient areas such as the Congo Basin, but also in other remote areas of high conservation value, local ecological knowledge is a valuable resource for tracking complex changes within socio-ecological systems, and local knowledge-holders can play a crucial role in understanding and managing those changes. Community-based observations can effectively complement scientific approaches, offering insights into ecological trends that would otherwise be difficult to detect through remote sensing or ecological modeling alone. Integrating this knowledge into conservation and climate adaptation strategies can improve policy responsiveness and effectiveness, particularly in under-researched ecosystems. While scientific efforts such as the CBSI or the SCPB are primarily geared towards the natural sciences, with a strong focus on atmospheric patterns, forest dynamics or satellite-based land-cover analysis, expanding their scope to incorporate local ecological knowledge as a rapid and cost-effective tool could contribute to filling existing research gaps and improving conservation outcomes in Congo Basin ecosystems.

3. Integrating indirect climate change impacts into adaptation policies:

Beyond the current silo approach that characterizes climate change mitigation, adaptation and conservation policies in the Congo Basin (and beyond), they should account for both the direct effects of climate change on species but also for the indirect impacts that arise from human responses to environmental shifts. While adaptation strategies play a fundamental role in alleviating the additional constraints posed by climate change impacts on livelihoods and human well-being, certain measures, such as agricultural expansion or increased reliance on natural resources, can exacerbate existing pressures on biodiversity. Conservation efforts must therefore incorporate a socio-ecological perspective, recognizing that human adaptation strategies may contribute to habitat loss, species decline and ecosystem degradation. Conversely, climate adaptation strategies should be designed to minimize unintended ecological consequences, ensuring a holistic approach to both biodiversity conservation and climate resilience.

4. Incorporating climate change considerations into protected area expansion under the 30x30 Framework:

The designation of new protected areas under the Kunming-Montreal Global Biodiversity Framework's 30x30 target (which aims to protect 30% of terrestrial and inland water ecosystems by 2030, CBD, 2022) must explicitly integrate climate change considerations. Indeed, findings from Chapter IV underscore that most areas projected to retain future climatic suitability for key species, such as *L. cyclotis*, currently fall outside the existing protected area network. Future conservation planning should prioritize climate refugia to ensure the long-term viability of species of high conservation concern.

The Congo Basin in the Anthropocene: Concluding remarks

Congo Basin rainforests, one of the most biodiverse and ecologically significant biomes on the planet, are currently undergoing profound and multi-scalar structural changes. These alterations are driven by an anthropogenic cocktail of habitat loss, natural resource overexploitation and the accelerating impacts of climate change. Despite their pivotal role in the Earth system, much of the complex dynamics within these forests remain inadequately understood. Consequently, the precise nature of ongoing changes remains uncertain, demanding heightened scientific attention. This is particularly critical as the Amazon Basin, which faces escalating anthropogenic pressures, including deforestation, increased droughts, altered fire regimes and biodiversity loss, exhibit signs of reduced ecological resilience. In this context, the significance of the Congo Basin is expected to grow in prominence, positioning it as a potential stabilizing force amid intensifying global changes.

Looking to the future, the geopolitical and economic landscape surrounding the Congo Basin is however also undergoing a significant transformation. As demand for raw materials such as oil, diamonds and coltan continues to rise, the Congo Basin is projected to become an increasingly important global supplier of these commodities. This places the region at the nexus of a complex paradox: while its ecological preservation is critical for maintaining global environmental stability, its exploitation for resource extraction is seen as essential for meeting the development needs of both local and global human populations. This duality encapsulates one of the most pressing sustainability challenges of the 21st century.

This thesis underscores the incredible urgency in advancing knowledge on the Congo Basin's ecological and climatic transformations. Across chapters, it documents the profound severity of currently ongoing climate change at multiple scales, the heterogeneous responses observed across biodiversity and habitat types and the substantial consequences for human systems, including adaptation challenges faced by local populations. Fieldwork conducted in the Lac Télé Community Reserve, an important Congo Basin site, revealed profound socio-ecological shifts that may be unfolding undetected in other floodplains or Congo Basin ecosystems. Several impacts identified - such as altered migratory patterns in fauna and reduced wild fruit production - have also been reported in other tropical regions, including the Amazon Basin, suggesting that ecological transformations are affecting seasonally flooded ecosystems globally. Looking into the future, the study also presents a strong, cross-scenario and cross-dataset signal of projected climatic suitability loss for a keystone megafaunal species, the forest elephant, in critical conservation areas. When future deforestation risk is incorporated, prospects for habitat suitability deteriorate further, emphasizing the urgency of integrating climate projections into long-term conservation planning. Given the forest elephant's critical ecological role in shaping forest structure and maintaining ecosystem functions, its decline could trigger cascading effects on ecosystem integrity and resilience.

Collectively, those findings contribute essential new knowledge toward understanding both current and future climate change impacts in the Congo Basin, filling major gaps in empirical data for this globally significant region. The insights generated also enhance comparative understandings of tropical forested and floodplain systems, offering relevant parallels with ecological changes observed in the Amazon and Southeast Asia. Across chapters, this study explored multiple approaches to addressing key knowledge gaps, integrating both local ecological knowledge at the biological community level in a specific site, and ecological modeling for a species-level analysis at the regional scale. Advancing climate-biodiversity research in the Congo Basin requires a sustained commitment to interdisciplinary, cross-scalar methodologies capable of bridging localized experiences and regional-scale patterns. Increased support for interdisciplinary research in the region is essential, serving as a critical pathway for generating actionable knowledge and informing more adaptive, inclusive, and resilient conservation strategies. Ultimately, this thesis underscores the increasing urgency of preserving the ecological integrity of Congo Basin rainforests - home to extraordinary biodiversity and rich biocultural heritage - not only as a regional necessity, but as a global imperative for maintaining planetary resilience in the Anthropocene.

Likouala-aux-herbes river meanders, Lac Télé Community Reserve. Photo by M.B.

Chapter VI

Research outputs and contributions

Key research outputs:

- **Milena Beekmann**, Sandrine Gallois, Carlo Rondinini. Uncertain future for Congo Basin biodiversity: A systematic review of climate change impacts. Biological Conservation, Volume 297, 2024, 110730, ISSN 0006-3207, https://doi.org/10.1016/j.biocon.2024.110730.

- **Milena Beekmann**, Célie Moungouya Moukassa, Carlo Rondinini, Alain Loumouamou, Andrea Lauta, Aida Cuni-Sanchez, Sandrine Gallois (2025). "We saw fish in the cocoa farm": Local observations of the impacts of climate change on biodiversity and livelihoods in the Lac Télé Community Reserve, Congo Basin (in review in **Ecology and Society**).

- **Milena Beekmann**, Nina Santostasi, Aida Cuni-Sanchez, Sandrine Gallois, Carlo Rondinini (2025). Shrinking climatic space: Implications for forest elephant conservation in the Congo Basin under climate change (in preparation).

- Katherine Meier, **Milena Beekmann**, Tiriel Lokota, Célie-Léoda Moungouyou-Moukassa, Bola Madzoké (2025). Fine-scale human-flood relationships in the Congo Basin: Ethnographic perspectives from the Lac Télé Community Reserve (in review in Philosophical Transactions of the Royal Society, as part of the special issue: "African tropical peatlands: their value and vulnerability").

Collaborative research outputs :

- Claire Vincent, Andrea Cristiano, Ivon Cuadros-Casanova, Michela Pacifici, Carmen Soria, Lisa Tedeschi, **Milena Beekmann,** Alessandra D'alessio, Pablo Lucas, Dario Nania, Carlo Rondinini (2024). The war in Ukraine is changing plausible future socio-economic scenarios leading to an unexplored outlook for biodiversity. Conservation Science and Practice, 6(9), e13056. https://doi.org/10.1111/csp2.13056

- Michela Pacifici, Claire Vincent, **Milena Beekmann**, Andrea Cristiano, Alessandra D'alessio, Claudia Forceni, Carlo Rondinini (2025). Mexico's interoceanic corridor creates an mezo-american island, threading biodiversity conservation (in preparation)

- Nina Santostasi, **Milena Beekmann**, Michela Pacifici, Alessandra D'alessio, Claudia Forceni, Carlo Rondinini (2025). Climate change impacts on terrestrial and marine mammal conservation: a comparative assessment (in preparation).

Conference contributions:

- 2024: Assessing climate and biodiversity changes in the Lac Télé Community Reserve, Republic of Congo, through a local ecological knowledge lens (talk). 7th European Congress of Conservation Biology, Bologna, 17-22 June 2024.

- 2024: Assessing climate and biodiversity changes in the Lac Télé Community Reserve, Republic of Congo, through a local ecological knowledge lense, CongoPeat project, 11-12 September 2024.

- 2025: Assessing climate and biodiversity changes in the Lac Télé Community Reserve, Republic of Congo, through a local ecological knowledge lense (poster). Student Conference on Conservation Science, University of Cambridge, 1-3 April 2025.

- 2025: Shrinking climatic space: Implications for forest elephant conservation in the Congo Basin under climate change. Second conference of conservation biology for early-career researchers, Society for Conservation Biology, Italy Chapter, 6-9 May 2025.

Research grants won:

- 2022: Belmont Forum Soils 2020 International Scholars Program, 8,000 $.
- 2022: Sapienza University avvio alla ricerca, 4,000 €.

- 2022: Sapienza University bando mobilità, 3,500 €.
- 2022: Rufford Foundation, 6,000 £.

International research experiences:

- 2022: Research stay at the Autonomous University of Barcelona, Institute of Environmental Science and Technology (ICTA-UAB), under the supervision of Dr. Sandrine Gallois (15-20/03/2022).

- 2023: Research stay at the Autonomous University of Barcelona, Institute of Environmental Science and Technology (ICTA-UAB), under the supervision of Dr. Sandrine Gallois (16-20/04/2023).

- 2024: Research stay at the Autonomous University of Barcelona, Institute of Environmental Science and Technology (ICTA-UAB), under the supervision of Dr. Sandrine Gallois (22/02-27/03/2024).

- 2024: Research stay at the International Environment and Development Studies Department, Norwegian University of Life Sciences (NMBU), under the supervision of Associate Professor Aida Cuni-Sanchez (16-29/09/2024).

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Supplementary material

Fine-scale human-flood relationships in the Congo Basin: Ethnographic perspectives from the Lac Télé Community Reserve

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The Likouala-aux-Herbes River and surrounding swamp forests of the northern Republic of Congo are described in scientific literature as a wetland forest system characterized by a bimodal flood pulse and widespread seasonal flooding. Recent advances in climatic and hydrological modeling of the Congo Basin and Cuvette centrale peatlands, moreover, position the Likouala region as a largely rainfed or ombrotrophic peatland. However, the experiences and adaptations to flooding by human populations occur at a more localized scale. This study presents comparative ethnographic data on flooding and seasonality from six villages within the Lac Télé Community Reserve, a protected area in the Likouala swamp forest biome, and the Republic of Congo's only community reserve. Our findings reveal how spatio-temporally variable flooding processes lead to dynamic patterns of socio-cultural diversity across the Reserve. Specifically, the origin, duration and extent of flooding is understood to be different between villages, driving village-specific cultures and livelihood cycles, adaptations, and vulnerabilities. The directional connectivity floods bring to the landscape also produces a North-to-South gradient of biocultural relationships. Across villages, flood dynamics have changed drastically over the last decades, with the year 2000 remembered as a particularly acute moment of hydrological change. Climate change, economic transitions and erosion of local knowledge systems appear to be straining long-standing adaptive frameworks within and between LTCR communities. This research emphasizes the importance of ethnographic data in understanding fine-scale human-environment interactions. We suggest that biocultural analysis at this scale - what we term the "hydrosocial patch" - is essential for effective landscape governance and could enhance future policy development, particularly in the context of climate change adaptation strategies.

Introduction

The Congo River Basin's hydrology is increasingly recognized for its critical role in the global carbon cycle and the ecosystem services it provides to human populations living in and around it (Dargie et al., 2019; Kitambo et al., 2022). However, the biophysical processes associated with Congo Basin forests remain exceptionally understudied, even as they face escalating pressures from commercial land-use changes (e.g., deforestation and forest degradation from logging, mining and other extractive industries), with the region's wetland forests particularly at risk from climate change-driven disruptions to seasonal flooding regimes (Biddulph et al., 2022). These combined threats - expanding industrial interests and global climate change - synergize with the lack of baseline environmental data to pose existential risks to the forest-dependent populations (human and non-human) of the region. The spatiotemporal variations in "*seasonal flooding dynamics, water level variations and vegetation types*" (Kitambo et al., 2022, p.1857) are among the characteristics of greatest interest to researchers leading the emerging efforts to "*transform our [scientific] understanding*" of the Congo Basin (CBSI, 2025). Most research prioritizes carbon storage and greenhouse gas dynamics, employing remote sensing and mathematical modeling at Basin-wide scales. While valuable, such approaches often simplify or homogenize ecological complexity and cannot speak to locally relevant biophysical processes occurring at fine scales. These researchers have continuously underscored the need to more deeply account for the "*heterogeneity of peatland hydrology across the region […] to understand the relationship between the river networks and the adjacent wetlands*", as well as need to extend ecological valuation of the peatlands to include understanding how they "*support local livelihoods and cultures*" (Biddulph et al., 2022, p. 11).

To address this critical knowledge gap, this study presents fine-scale ethnographic data on local understandings of and adaptations to hydro-climatic dynamics and variability from six villages of the Lac Télé Community Reserve (LTCR), a protected area in the Likouala Department of the Republic of Congo. By documenting local ecological knowledge, this research aims to elucidate the relational and historical dimensions of hydrological processes, particularly the seasonal flood pulse. Our data, collected through semi-structured interviews and participant observation, provide insights into both village-specific and catchment-wide mechanisms by which communities inhabiting a single river-floodplain wetland observe, interpret and respond to dynamic hydrological processes. Through these data, we highlight the flood-driven diversity in cultures and livelihood cycles of LTCR's human communities, contributing to understandings of peatlands as unique biocultural systems whose conservation requires accounting for the entanglements and reciprocity between biophysical and socio-cultural processes (Thornton et al., 2020). We also emphasize the complexity of local environmental knowledge and value systems at and across LTCR, valorization of which is necessary for equitable and sustainable governance solutions (Zafra-Calvo et al., 2020).

Methods

Study site and communities

The Likouala region, part of the Cuvette centrale depression in the central Congo Basin is characterized as a seasonally flooded swamp forest. In 2017, the world's largest expanse of tropical peatlands was discovered in the region (Dargie et al., 2017), catalyzing a major uptick in scientific interest and investment in the region. The Lac Télé Community Reserve (LTCR) is located along a section of the Likouala-aux-herbes river (LAH), a tributary of the Oubangui River and part of the broader Congo river system (Fig. 1). The LAH remains a free-flowing and ecologically intact river-floodplain system, lacking major anthropogenic modification or development. The river exhibits a bimodal annual flood pulse, creating four distinct seasons commonly referred to as the "big" and "small" rainy and dry seasons. However, past scientific research in the LTCR has often chosen to recognize only the low-water season and the high-water season (e.g. Poulsen & Clark, 2002). Annual average rainfall ranges between 1.000 and 1.800 mm, and the mean annual temperature is 25.6°C (Bondeko, 2016).

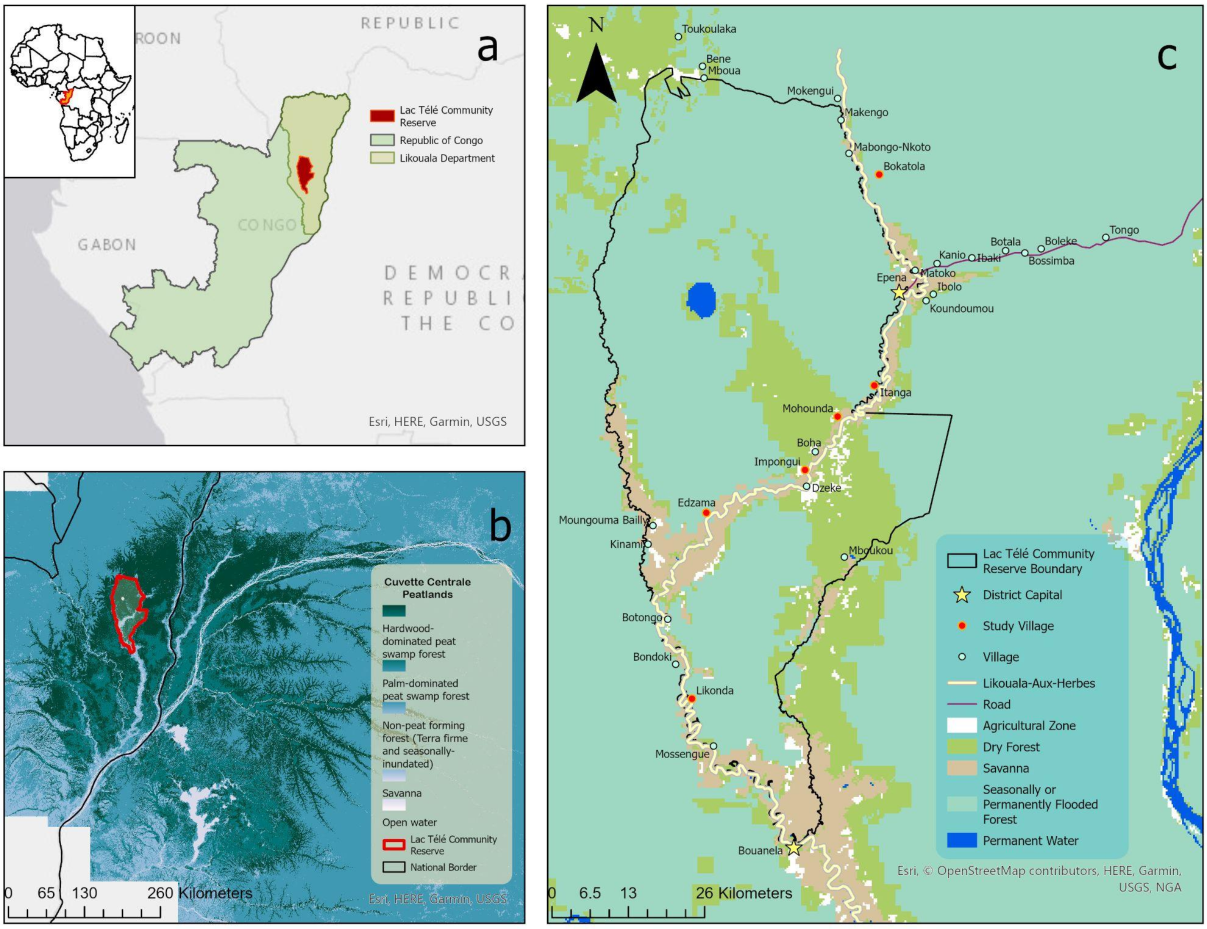

Figure 1: Localization of the study site with ecological zones and village communities: a. The Lac Télé Community Reserve located in the Likouala district of the Republic of Congo. **b.** Localization of the LTCR within the Congo Basin's Cuvette centrale peatlands (peatland probability map from *Crezee et al. (2022)*. **c.** Protected area boundaries, village communities along and around the Likouala-Aux-Herbes river, and basic landcover classes (ESA GlobCover 2009). Maps produced by KM.

The LTCR was officially gazetted as a protected area in 2001 and is managed by the Congolese Ministry of Forest Economy and the Wildlife Conservation Society (WCS). As the Republic of Congo's only community reserve, the protected area encompasses 31 villages (~20,000 people) distributed from North to South along the riverbank. Throughout most of the LTCR, travel is limited to boat - only one road connects the northern village of Epena to the nearest market center, Impfondo. Ethnically, the LTCR's population is considered to be functionally homogeneous, with over 90% identified under the umbrella category of Bomitaba, a Bantu group formalized during the French colonial period when small, factious, forest-dwelling clans were relocated to villages along the navigable LAH for easier control and taxation. Much of the remaining 10% of LTCR's population are composed of hunter-gatherer Aka groups as well as immigrants from surrounding regions (Poulsen & Clark, 2002). The LTCR is ecologically, politically, and culturally bisected. Ecologically, a northern hardwood swamp-dominated "sector" and a southern seasonally flooded forest-dominated sector are separated by a large, central *terra firma* corridor (Poulsen & Clark, 2004, Fig. 1). Politically, the LTCR spans two administrative districts - Epena and Bouanela - with eponymous village centers respectively falling in the northern and southernmost reaches of the LTCR. Though landscape managers qualify the Bomitaba as a unified group, linguistic research and socio-cultural indicators (such as traditional dances and burial rituals) show that the eco-political divides align with cultural sub-group divisions within the Bomitaba, largely between the Reserve's North and South; in the central village of Itanga, for example, residents speak a dialect blending northern and southern variants (Leitch, 2009). Several of our local interlocutors confirmed that individuals from southern villages can have trouble understanding the Bomitaba language spoken in more northern villages, and vice versa.

LTCR communities depend upon the forest's and river's natural resources for their lives and livelihoods. Living in a wetland ecosystem, LTCR residents have a heavily fish-dependent diet and economy. However, subsistence activities available to people in each village are diverse and often distinct. Nearly all men engage in a seasonal mix of fishing and hunting. Women also fish and are typically the primary managers of agricultural fields. Fishing rights and access are traditionally governed by customary tenure systems wherein each family maintains exclusive control over designated ponds and specific portions of the river. Agriculture is practiced in a traditional swidden cycle and, since the availability of dry land is limited, most people focus their efforts heavily on cassava cultivation, the main staple starch of the region. Other common crops include plantains, avocados, sugar cane and oil palm. In certain villages, cocoa is also cultivated for commercial purposes. Other subsistence activities, like the gathering of non-timber-forest products (NTFPs), are also practiced by both men and women. Important resources include tree species used in house construction, wild fruits, mushrooms and caterpillars. Several LTCR natural resources are also important commodities in wider economic trade networks, key among them being smoked fish, cola nuts, honey and dwarf crocodiles. Independent of the permanent Aka communities within the LTCR region, groups of "Yaka" hunter-gatherers migrate seasonally into the LTCR swamp forests from the neighboring Sangha region where they move between Bomitaba villages in search of these commercially-valuable resources (see Lewis, 2002).

Data collection

The data utilized for this study derives from two independent ethnographic studies conducted between January and December 2023, in six villages: Bokatola, Itanga, Mohounda, Impongui, Edzama and Likonda (Fig. 1). The two projects were included as part of the doctoral theses of authors K.M., M.B. and T.L.N. Authors K.M. and T.L.N. formed one research team and worked in Impongui, Edzama, and Likonda (study one) while authors M.B. and C.M. formed the second and worked in Bokatola, Itanga, and Mohounda (study two). Author B.M., a Bomitaba native and site ecologist for WCS, assisted the other authors in the development and realization of their respective field studies. Study one focused on great ape conservation and natural resource-use in reserve communities while study two centered around local observations of and adaptation to climate change. As social scientists working contemporaneously on complementary topics, we worked together to strategically select our study villages to avoid overlap while representing the full spectrum of socio-ecological conditions across the LTCR, ensuring representation of its northern, central and southern zones. Our data collection methods included semi-structured interviews (n=196 informants), focus groups (n=11 groups), and participant observation where we lived in each focal village for 6-8 weeks, engaging in the daily life of village communities. After meeting with village chiefs, elders and cultural leaders and gaining approval for work in each village, we employed a stratified random (study two) or snowball sampling approach (study one) to recruit interview respondents who were men and women ages 18 and above. Interviews typically lasted between one to two hours. Focus groups were stratified between men and women and averaged around 20 participants. We asked questions from questionnaires that were pre-approved by the human subject ethics committees of our respective institutions. At the start of each interview, we gained the written or verbal consent of participants after an explanation of the project aims, data management plans, conditions of anonymity, potential participation risks and participation compensation. Interviews were conducted in French, Lingala, or Bomitaba, using local interpreters where required. Given the consent of the participant, interviews were recorded on handheld audio recording devices, and we took detailed notes during the interviews.

Data analysis

Interviews and field notes were transcribed by authors K.M., T.L.N. for study one and M.B. and C.M. for study two. For each study, transcripts were coded and analyzed for major themes. Our respective research objectives collectively encompassed understanding diverse aspects of human-environment relationships, traditional to current-day land-use patterns and socio-ecological changes. We combined data from our two datasets concerning weather, seasonality and flooding and re-coded for commonalities and divergences by village. The agentive role of flooding in shaping fine-scale biocultural dynamics across study villages emerged independently in both of our datasets. In the following section, we detail our results and discuss their relevance to ongoing conservation and governance efforts within the LTCR and across the broader peatland forests of the Cuvette centrale. Village-specific data are distinguished by the village from which they originated.

Results

Seasonal flooding dynamics and hydro-climatic variation across the LTCR

The regularity of the seasonal flood-pulse in river-floodplain systems like that of the LAH, is thought to be the driver behind the system's ecological diversity and productivity (Junk & Wantzen, 2004). Though the LTCR ecosystem at the Basin-level has experienced a regular flood-pulse for at least as long as human memory can recall, the LTCR's flooding regime is highly variable and spatio-temporally dynamic. Moreover, this variation corresponded to differences in how people experienced seasons within and between reserve villages.

Flooding in the LTCR varies significantly across time and space, shaping inter-individual and inter-village variation in seasonal perceptions perceive and experience seasons. While four seasons are broadly recognized by LTCR populations, the timing, duration, and interpretation of seasonal shifts are often understood differently. Figure 2, a seasonal and activity calendar for each village (data averaged from individual interviews for villages in study one and from focus group interviews for villages in study two) shows the inter-village diversity in perception of seasonality. At Impongui, a *terra firma* forest village that never floods, more than half of our respondents (n=10) recognized only two or three seasons, omitting the small dry season most frequently. In contrast, Edzama residents, located around 20 kilometers South and surrounded by hardwood swamp forest, most reliably listed all four seasons. More than half of the respondents there (n=11), however, placed the small dry season during the months typically considered to be the long dry season (January-March). From these collective inter-village data, it becomes apparent that the three northern villages have a more uniform understanding of seasonality suggesting that variability in flood timings (seasonality) becomes more pronounced further down the LAH. Village activity budgets, grouped into the broadest livelihood categories and mapped onto each seasonal calendar as being "low" or "high" during that period, represent the intensity of subsistence activities by month and season. While the Reserve's people universally diversify their livelihoods relative to seasonality (see "The river-peatland network"section), it is also important to observe the inter-village diversity present here as well. Likonda and Bokatola, while at opposite ends of our study area, seem to have comparably bifurcated activity cycles which probably reflects the fact that, of our study villages, these two experience the highest degree of seasonal flooding in and around their villages. Itanga, like Likonda, is located in an area of seasonally flooded forest and these two villages have the most similar seasonal calendars between our northern and southern sites. However, unlike Likonda, Itanga is also proximal to the large strip of *terra firma* forest in the Reserve's center, providing its residents access to a more diverse array of ecological conditions and resource environments. This difference likely explains their contrasting activity budgets. Similarly, Mohounda and Impongui, both positioned on the large strip of *terra firma* forest, exhibit exceptionally divergent activity budgets, likely reflecting Impongui's proximity to the *terra firma*'s edge and thus their lesser reliance on seasonal hunting due to year-round access to river and forest fishing areas.

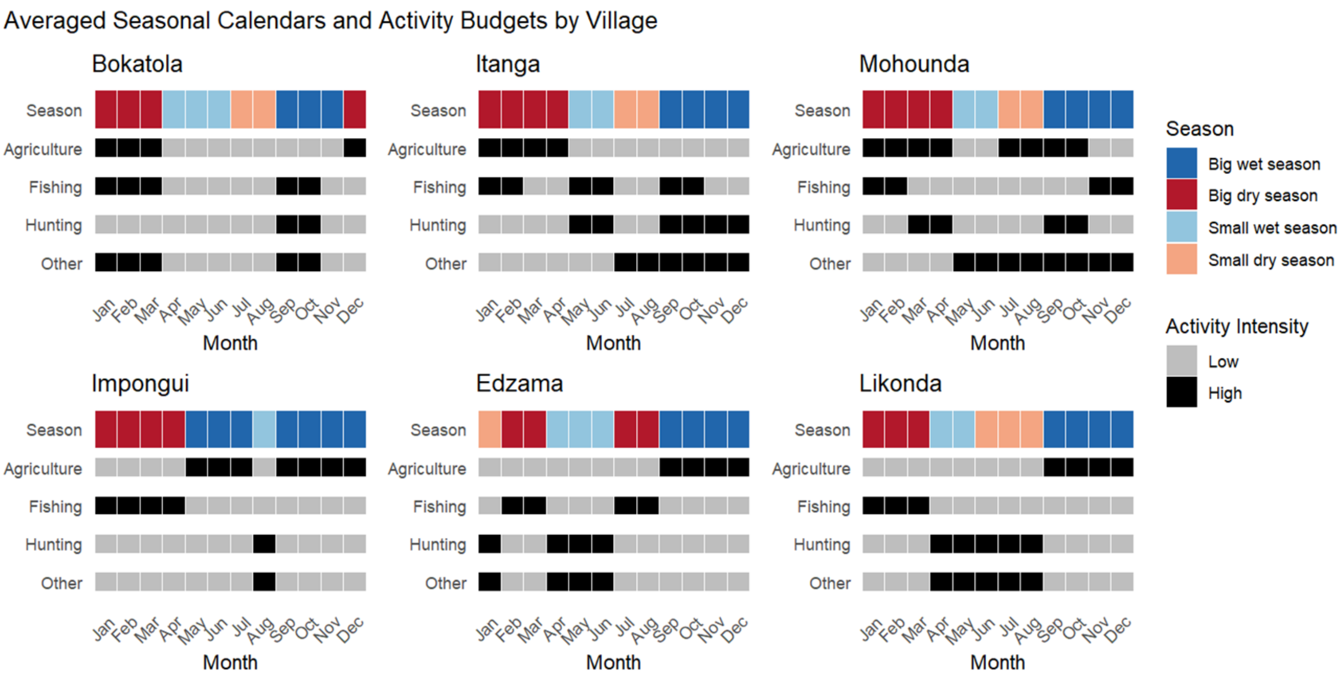

Figure 2: Seasons and activity budgets averaged Per village: Plotted in color is the relative timing of each season by month as recognized collectively by the residents of each study village. Below, the intensity of livelihood activities is mapped to corresponding seasons. Category "Other" mainly includes the collection/gathering of non-timber forest products like raphia fronds, cola nuts, honey, etc.

There is further diversity in local understandings of how floods begin and then permeate the LTCR landscape. In the northern part of the Reserve, residents cite rainfall over forested areas as the primary source of flooding: "*it takes maybe one week for the rains to reach here* [Mohounda] *from the Kabounga lands* [region north of LTCR]. *There are two canals there, one to the Moungouma Bailly* [river] *from Toukolaka, and another going to the Likouala-aux-herbes* [river]. *The water here comes from Cameroon via the Tonga river, which flows into the Likoualа-aux-herbes near Matoko. The waters of the Oubangi flow directly into the Congo river. If it flooded there, it is going to flood here. The river never floods the village. It's mko* [described as a type of sub-surface water that runs through underground channels] *that floods it. It meets the water rising from the river. Mko flows from August onwards. You can see it at the village port, it's light-colored*" (Mohounda). In contrast to this quote, a respondent from Impongui, a village slightly further south, didn't see rainfall as driving flooding: "*the seasons are determined by* [river] *water level, not rainfall… There are different kinds of rain. One kind is when the rain begins at 5am and continues until late the next day.*" In Edzama, villagers understand the forest and water levels to rise at the same time, neither outpacing the other; the river rising to flood the outer band of riparian forest while groundwater rises to saturate the inner swamp forests. Lastly, in Likonda, several people described a third flooding regime where the river gradually rises and eventually floods its banks, funneled into surrounding forest via terrestrial channels, "moloukou" (not subterranean like the mko channels of Mohounda). Well-trodden forest elephant trails through Likonda's seasonally flooded forest territory, intersect with the natural flood channels, further complicating the patchwork flooding of this village-forest territory (Meier, pers. obs.). The forests surrounding Likonda being seasonally flooded, they boast *terra firma* ground. However, several respondents in this village insisted on their ground being distinct from the *terra firma* in the Reserve's central strip: *"When floods leave the north, they fill the Cuvette where we are. At Likonda, we are at the bottom of the basin. Here we have terra firma but not the same terra firma as Impongui. Impongui is higher up in the basin […] Here, water only enters at our corners."* Another Likonda respondent noted how, even right across the LAH from the village, the flooding regime and ecological communities are different: "*on the other side of the river, there are different types of trees. It doesn't flood easily there. Here the trees are aquatic* […]. *We don't have gorillas on this side of the river because their favorite foods* [Raphia spp.] *aren't here*." The perception of a North-to-South flood gradient was common amongst respondents in our southern villages "*floods start at Epena and trickle down. The North and South have opposite seasons"* (Likonda). Figure 2 shows that the northern villages (top three) and southern villages (bottom three) show relatively similar seasonal calendars. However, looking at the breakdown of activity levels by season, it is evident that villages in the North engage in agriculture and fishing during the first half of the year with hunting and gathering non-timber forest products (activity category "other") occurring more frequently during the latter half of the year while the reverse pattern can be seen in the more southern villages. Taken together, it is apparent that not only are local understandings and perceptions of flooding and hydrological processes across the LTCR tightly linked to livelihood cycles, but that each LTCR village is subject to specific flooding processes linked with micro-scale climatic and topological conditions, all corresponding to unique ecological assemblages. Moreover, the existence of distinct, village or area-specific words reflects distinct village-environment relations and localized forest knowledge (Table 2). For example, the words "*metele*" (used in Bokatola) and "*miyela*" (used in Itanga and Mohounda) refer to a locally recognized period of stagnant water, which can occur during the dry or wet season and is considered by residents of these villages to be a climatic anomaly. In our southern villages, we did not encounter these terms and concepts, signaling fine spatial variation in the hydrological processes of the region. Despite the fine scale variation evident in these quotes, our respondents - such as the one first quoted in this paragraph - display strong understanding of the regional scale hydrologies driving local flood seasonality: "*everything here is connected by rivers and floods, all the way to Cameroon*" (Edzama).

Significant flood events remembered included those in 1977, 2000, 2011, and 2020. In the South, respondents viewed "bad" or extreme floods as occurring on roughly a 10-year cycle, although this statement was not shared as broadly in northern villages. In these villages, however, 1977 was not cited as one of the bad flood years. As references to this flood year in the North were sometimes accompanied by memories of State-sponsored aid (in the form of rice and oil shipments), this North-South discrepancy may reflect political conditions: the southern district of Bouanela had yet to be formed and was much less accessible to administrators than Epena and the more northern reaches of the LAH. Notably, many respondents perceived flooding in village areas as a relatively recent phenomenon. During the colonial formation of LTCR's villages, all were localized on "islands" of dry land. Only since around the year 2000, respondents across villages asserted, had flooding begun to breach village boundaries, reaching unprecedented spatial extents. This could explain why no LTCR natives have evolved one of the most common adaptations to seasonally flooded life - building on stilts - seen in communities inhabiting similar floodplain ecosystems across the tropics including the peatland forests in neighboring Democratic Republic of Congo (B.M., pers. comm.; for reference, see photo in CongoPeat, 2023, p. 21); villagers at LTCR had only recently been exposed to extreme flooding in their villages. In further support of this assertion, it is common to see seasonal fishing camps located along the edges of the Mandoungouma river (a tributary of the LAH) built on stilted platforms above the water (Fig. 3) suggesting that LTCR inhabitants possess the capacity to construct on stilts but did not evolve the need to use it in village settings. Across study villages, residents had a variety of techniques they used to determine the severity of a flood event. Across villages, the flooding of cassava fields - typically placed in the least flood-prone areas - signaled a particularly bad flood. In Bokatola and Impongui, residents track the progression of floods by marking the river levels on the trunks of flooded riverside trees. In Edzama and Likonda, hunters relayed that they knew a bad flood had occurred when they found animals drowned in the forest. Edzama residents recalled the unprecedented need to use boats to traverse their village during the 2000 floods.

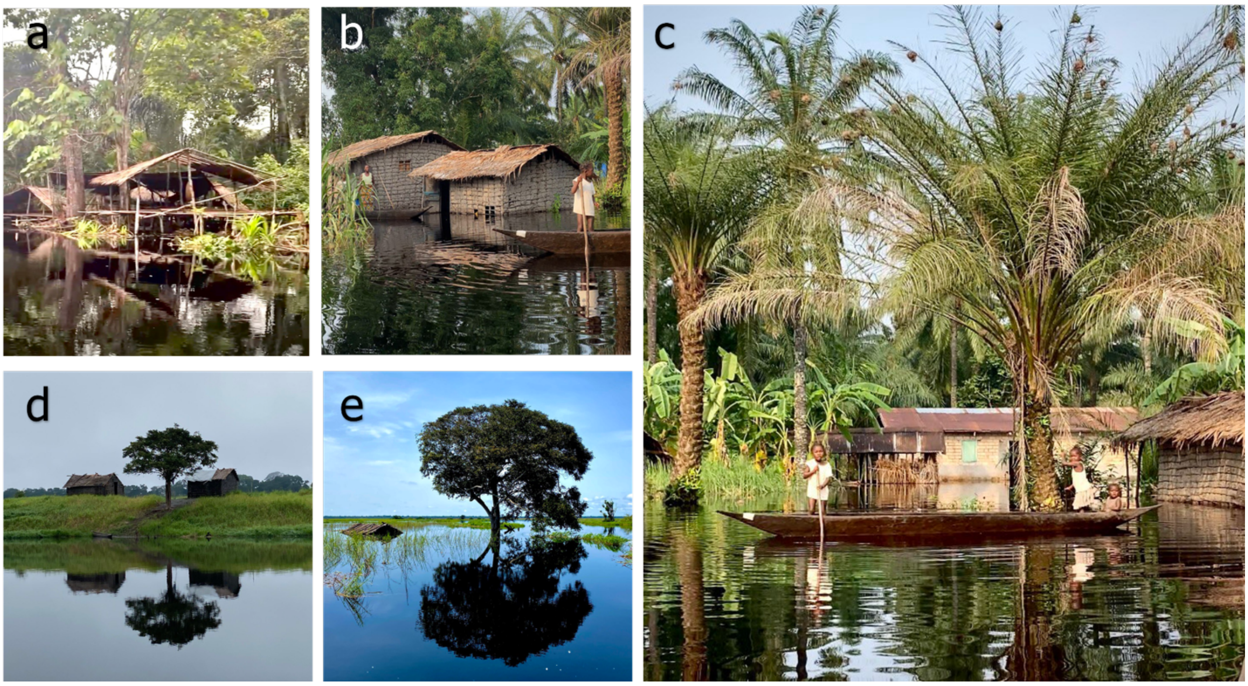

Figure 3: Examples of village and fishing camp flooding: a) A seasonal fishing camp built on stilts along the edge of the Mandoungouma River (July 2022). **b and c)** Young children using a pirogue to travel between houses during flooding in the village Mabongo-Nkoto, northern LTCR (July 2023 during the unprecedently early big wet season). **d and e)** Seasonal fishing camps along the LAH during low and high-water periods (March 2023). Photo e. May 2023. Photos by K.M.

Across all study villages, respondents underscored the deviation of present-day flooding from the normal flooding cycle, with floods occurring more frequently, lasting longer, and reaching unprecedented levels. Our field period, 2023, featured one of the most exceptional flooding events in remembered history: "*the water surprised us all*" said a Likonda resident of the floods that started in April, 2023 - four to five months ahead of schedule. *"We are in May. This should be the short rainy season but it is instead like the big rainy season!"* (Edzama). He went on to describe the far-reaching effects of seasonal and environmental change across the reserve: *"the river used to be very deep. Boats could arrive to Epena even in the long dry season. Now the river has lost its value […] It's now people who provoke the floods. There used to be respected burning periods. Now people burn however they want."* (Edzama). In several villages, residents recognized the cyclical process of unpredictable floods leading to droughts, leading to uncontrolled burns of riparian and savanna areas (a practice that has a long local history and specific traditional regulatory processes (Kirkby, 2014)) which, in turn, leads to increased important riverbank erosion and the filling-in of the LAH. A shallower river and more extreme water recessions during low-water months means never-before-seen impediments to river-based travel/trade on top of more fundamental challenges like lack of access to drinking water.

Today, as floods increasingly penetrate villages across LTCR, flooding experiences shape distinct village identities and politics. In each of our three southern villages, residents insisted that the degree of flooding in their village was unique compared to surrounding ones, lending them superiority or advantage particularly regarding access to dry land. Likonda residents compared themselves to residents of Edzama, Bondoki, and Epena: *"Edzama floods! Where we live, that's a ruisseau* (Table 1). *It's different. Epena floods but here in Likonda, it's only in the corners. At Epena, you go live with your neighbors during floods* […] *At Bondoki, their forest has water everywhere. Here is the dry forest"; "We don't flood here. In the forest it floods but our fields don't. Other villages come to use our fields."* Edzama residents noted how, despite their greater susceptibility to flooding, the predictability of floods and the importance of ancestral connections to land made life there tenable: "*How do we survive? We are from here. It's our ancestral home. Edzama doesn't flood randomly like it does at Kinami, for example*;" "*Our ancestors left us here. We cannot leave, we must respect tradition. You can always find dry land to live on*." Impongui residents compared themselves to Epena: "*the difference between Epena and Impongui is we can cultivate our fields during the flooded period. At Impongui, life is better and simpler because there are no floods;" "At Botongo and Mosingi, people were displaced by floods in 2000, but we were able to stay."*

The river-peatland network and its value to local livelihoods and vultures

Since seasonal flooding in flood-pulse river systems like LTCR's drives the fine-scale spatio-temporal distribution of ecological diversity and productivity, the dynamics of flooding across the LTCR landscape exert significant influence on what resources are available to local people, when, and where. As LTCR's human population is considered subsistence-based or natural-resource-dependent, communities exhibit Reserve-wide adaptations to their uniquely water-dominated environment as well as diverse, seasonal, and flood-dependent livelihoods and cultural practices.

LTCR inhabitants have highly mobile yet territorial relationships to place. From an early age, children are trained in essential water-based survival skills, including swimming and the operation of dugout canoes, which are integral to transportation and subsistence activities (Fig. 3). Canoes are typically custom-made, with paddles designed to individual specifications. Across the LTCR, settlement distribution is primarily governed by ancestral land tenure and long-term place attachment: *"How do we survive? We are from here. It's our ancestral home;" "Edzama doesn't flood completely and our ancestors are here. We wouldn't leave!"* (Edzama). Similar sentiment was widely expressed in all study villages, including those subjected to more intense floodings, such as northern Bokatola. Itanga residents, for example, collectively decided to relocate in 1962 - spurred by factors including the water stagnation, challenge of needing to use pirogues for basic travel, and deterioration of most earth-based homes brought about by prolonged flooding. They did so, however, only within the limits of their ancestral territories (see Kirkby, 2014, p.68, for a visualization of village "terroirs"). In several villages, however, respondents described the historical practices of using termite mound deposits (called "*bangoumou*" in central areas; see Table. 2) to elevate housing foundations and maintain dry zones for hearth placement. This method remains in use, albeit progressively substituted by contemporary construction using materials such as bricks, used to elevate living spaces, furniture, or beds. In northern villages, respondents reported that a minimum height of four bricks was now considered essential to mitigating flood impacts.

All observed households maintain diversified livelihood portfolios that are closely synchronized with hydrological variability, integrating agriculture, fishing, hunting and NTFP collection. Agricultural practices are both spatially and temporally structured around flood dynamics. Respondents involved in agriculture (mostly women) described a prioritization approach to cassava harvesting, wherein fields most vulnerable to flooding are harvested first, while crops in drier zones are left to mature longer. In areas subject to frequent and severe flooding, all cultivated fields are dedicated to short-cycle crop varieties to mitigate potential losses. A small number of respondents in northern villages also mentioned the historical use of raised agricultural fields as a flood adaptation strategy, a technique that has been documented by researchers in floodplain communities neighboring the Bomitaba (Comptour, 2017; Rodrigues et al., 2020). While flooding is often cited as a limiting factor for cassava cultivation due to crop loss and restricted field availability, it is simultaneously recognized as an essential agroecological process for nutrient cycling and soil fertility restoration.

Flood variation and corresponding fish movement and reproductive ecologies also dictate subsistence and commercial fishing patterns. Fishing techniques are highly stratified by flood phase and vary across the LTCR with techniques adapted to fluctuating water levels and fish migration patterns. The big dry season constitutes the principal fishing period, as fishers capitalize on flood recession to maximize catches in both the river and savanna/forest pools. During this period, men and women temporarily leave the village to engage in intensive fishing operations at family-owned fishing camps, located either along the main river channels or within the forests. In Likonda, several respondents mentioned the near abandonment of the village during low-water periods: "*Sometimes only five or six people remain in the village. Animals then aren't scared away by the noise of the village. One time, a village dog was eaten by a python that came right into the village*." During the big dry season, when water levels are low, fishers employ *kokopa*, a manual removal of water from ponds to concentrate fish, a practice historically performed with the *ekoumba*, a tub woven out of raphia and operated by four individuals. Women commonly used *eyika* baskets (Itanga) in small ponds and riverbanks, alongside *mileke* and *molo* fishing traps. Communal techniques include the *okala* trap, used to capture fish, caimans, and snakes in rivers and large ponds, as well as large *motresse* nets. *Mbilo* fishing involves clearing vegetation to channel fish into designated catchment areas. During the big wet season, when water levels are high, fishers shift to *ndobo* hook and line fishing, a technique for individual subsistence. Nets remain in use year-round but are adjusted in mesh size and placement based on water levels and fish migration routes. The big dry season represents a critical economic period, characterized by heightened fishing activity and expanded trade networks, increasingly integrated into regional and national commercial circuits. A poor big dry season, characterized by low fish catches due to inadequate water recession, can severely impact household finances, as many rely on fishing income to buy food stables such as oil and salt, cover education costs, access healthcare, and buy essential household goods like soap.

Seasonal floods expand peoples' access to remote and otherwise inaccessible areas within their traditional territories. Thus, in high-water seasons, gathering and hunting of staple and commercial forest resources increases (key resources include *Raphia* spp., cola nuts, *Gnetum* spp., mushrooms, liana, and Marantaceae spp.). Hunting activities across reserve villages often peak during the high-water season, when flooded landscapes concentrate wildlife, making tracking and capture more efficient. The dry season, however, can also facilitate hunting in areas adjacent to water sources. Our interlocutors described historical hunting with spears and nets (*bokila*), often requiring group or village-wide coordination to capture game. As firearms have become more prevalent, however, hunting has become a more individualistic and unregulated behavior. Water levels also influence logistics and material transport, creating temporary waterways that improve movement across the landscape. Seasonal shortcut routes, often named after significant locations, facilitate trade, family visits, and participation in cultural rites. Seasonal floods, most importantly, are widely seen to provide an ecological "equilibrium," allowing animal populations, fish especially, time and space to reproduce. Though fish are harder to find during the flooded season when they spread out across the watery landscape, fish from the forest are considered more nutrient dense than those caught in the LAH. Moreover, this period also corresponds to a high production period for other staple food resources such as safou (*Dacryodes edulis*, a fruit tree species native to the Congo Basin) and edible caterpillars. Transporting of heavy construction materials (specific species of hardwood trees, for example), is made easier by water-based travel through flooded forest areas and the duration of travel times between villages (by boat along the LAH) is greatly reduced during the flooded season, facilitating inter-village social and material exchange.

In northern villages, respondents emphasized the historical role of food preservation technologies to mitigate periods of food scarcity during peak flood periods. Traditional fish preservation methods include smoking or salting and sun-drying. Cassava, meanwhile, is fire-dried after peeling off the outer skin, placed in woven palm baskets (*mokota* in Itanga), and submerged in the river for gradual consumption. In central villages, large storage jars (*ediba*, referred to as "freezers") were used for both fish and cassava. Due to villages' increasing market integration, traditional food preservation practices are in decline as any surplus is sold for cash rather than stored: *"conservation was an old practice; these days, we sell everything"* (Bokatola). However, with increasing market integration, new materials and methods for food acquisition and preservation are emerging. In several of our study villages, fishing with soap was said to be a practice increasingly taken up by village youth and non-local fishermen coming from across the border in Democratic Republic of the Congo, allowing them to catch more fish at one time but contaminating the surrounding water in the process. In southern villages, we also observed fish sellers in multiple villages spraying their mallets of smoked fish - destined for trade as far as Brazzaville and into surrounding Central African countries - with a high-potency herb/pesticide called "Sniper" that, in other nearby countries, has become popular as a means of suicide. More LTCR residents are prioritizing short term commercial gain as flooding patterns and resource availability becomes less predictable, synergizing with deteriorations in traditional resource governance mechanisms and socio-economic conditions.

Overall, respondents expressed conflicted sentiments over their lives and livelihoods in LTCR's seasonally-flooded swamp environment. Water's predominance in the LTCR socio-ecological system presents both benefits and challenges. On the one hand, they feel well-adapted, having inherited and refined a wide range of livelihood strategies and having access in each village territory to diverse micro-habitats and associated natural resources. On the other hand, many voiced concerns about the increasing unpredictability of floods: *"the water forces us to work at a certain pace, and there are the disruptions of the seasons*" (Itanga). Beyond hydrological uncertainty, respondents highlighted broader socio-ecological shifts, including the intensification of natural resource harvesting, increased fire frequency, and the erosion of customary practices including collective resource governance, reshaping traditional food security strategies. In Bokatola, for example, a pond once considered spiritually significant is now actively exploited: *"it used to be a site of power, but now we neglect those traditions."* A respondent in Impongui noted how the colonial introduction of cacao cultivation - an economy that Reserve managers are now attempting to revitalize as an alternative livelihood project in several reserve villages - drove the loss of traditional forest fishing practices: "*we used to fish in forest pools during the big dry season but this practice doesn't exist now because of the introduction of cacao. Now during that season, people need to arrange their cacao fields, then harvest the fruits in the big rainy season."*

Discussion and conclusion

This study represents one of the first ethnographic investigations - incorporating unstructured qualitative data and prolonged participant observation - in the LTCR. The small body of research pertaining to the LTCR includes (mostly unpublished) colonial-era reports documenting aspects of Bomitaba culture along the Likouala-aux-herbes river (e.g. Patriat, 1956), landscape-scale institutional reports (e.g. USAID, 2017), and sporadic academic works which have largely focused on the Reserve's more accessible northern and central sectors and engaged either ecological or qualitative survey methods (Evans, 2014; Kalan et al., 2010; Kirkby, 2014; Leitch, 2009; Ndzana Biloa et al., 2024; Poulsen & Clark, 2004). Our ethnographic work, encompassing six villages across the 4.400 km^2 reserve, better captures the full spectrum of socio-ecological dimensions within the LTCR from North to South, and is hence distinctive in its method and scope, both within the Congo Basin peatland literature

(Comptour et al., 2016; Harms, 1981), and the broader human-wetland scholarship from around the world (Dewan, 2021; Haller et al., 2013; Harris, 2005; Junk et al., 2010; Langill & Abizaid, 2020; McGregor et al., 2010; Pyke et al., 2018; Sasaki et al., 2007; Thornton et al., 2020).

Our findings reveal both overarching patterns and fine-scale variations in how communities within the LTCR interpret and experience flooding seasonality. Annual flooding exhibits spatial and temporal heterogeneity, generally progressing along the LAH from North to South but penetrating each village-forest system in unique ways. During the colonial period, each village was established around small areas of unflooded ground amidst the larger seasonally flooded peat swamp ecosystem. Since around the year 2000, however, more and more communities have been experiencing floods that inundate their villages partially or completely.

River ecologists recognize that river-floodplain networks can be broken up into distinct (but continuous) "*hydrogeomorphic patches*," each with its own "*size, vertical and lateral shape, internal structure/hydrological complexity,"* and other components of *"biocomplexity*" (Thorp et al., 2006, p. 126). This complexity - driven by the flood-pulse - in turn determines the system's productivity and ecological diversity. In such systems, consequently, socio-economic parameters favor human resource-use patterns that are equally diverse and seasonally flexible (Junk & Wantzen, 2004, p. 124). Our findings support these previous understandings of river-floodplain systems and suggest the extension of the hydrogeomorphic patch to include contingent biocultural variation - a division of the LAH into discrete but relational "hydrosocial patches" or zones.

At LTCR, livelihoods are highly flexible, with few individuals relying on a single mode of subsistence. Instead, most engage in multiple activities, dynamically shifting resource dependencies in response to the seasonal flood pulse. While the dry season is preferred for food security, fish being more easily available, the flooded season is valued for house construction and forest-based fishing. Floods characterized as "bad" result in the inundation of typically dry areas such as cassava fields, villages, and homes. Mobility is a key adaptive strategy during flood events, yet ancestral ties bind people to their natal villages and forest territories. Recently, flooding patterns have shifted with earlier flood onset and prolonged droughts. Despite the challenges, seasonal floods are widely recognized as ecologically beneficial, supporting fish populations and nutrient distribution. Inter-village variations in flood knowledge and experiences are largely influenced by fine-scale hydrological regimes: while some villages remain unaffected by floods, others experience annual inundation or extreme flooding, particularly in the northern sector. This results in differential flood vulnerability across villages, as well as divergences in flood memory. While northern residents recall more severe floods in earlier decades, this likely reflects greater historical state presence in Epena.

Across themes, accelerating socio-ecological change is evident, shaped by both climatic and socio-economic shifts. A decline in traditional governance structures has led to the erosion of communal resource management practices, including burning, hunting and fishing (e.g. Kirkby, 2014). Market integration and conservation management-driven economies increasingly shape local livelihoods, pushing local communities to seek increased income sources, and leading to, for example, increased forest clearing for commercial manioc production or the devaluation of fruit species, which holds primarily subsistence value. Unsustainable fishing practices, (e.g. fishing with soap), yield short-term economic benefits but contribute to long-term environmental degradation. Those socio-ecological changes are further amplified by disruptions in the LTCR seasonal flood pulse. Our observations suggest that long-standing adaptive frameworks within LTCR communities are under increasing strain due to climatic shifts, economic transitions, and the erosion of knowledge systems. While demographic variables such as age, gender, and occupation influence individual observations related to flooding and environmental change, a detailed examination of these factors fall beyond the scope of this study.

Policy and governance implications

Recognized as "natural climate solutions," wetland ecosystems, particularly peatlands, are increasingly at the center of scientific concern amid the global climate crisis (Dewan, 2021; Scaramelli, 2021). However, their unique hydrological dynamics make them highly vulnerable to Anthropocene-driven changes. This growing fragility has intensified the urgency to understand and value the world's remaining wetlands, particularly those of the Congo Basin. Pursuing a singular, climate-centric research agenda, however, risks oversimplifying or neglecting the fine-scale human-environment interactions that both shape and are sustained by wetland ecosystems. This reductionist approach to research and the resulting top-down policies that it informs have been shown in other wetland systems to have negative impacts on socio-ecological resilience such as reduced adaptability and greater uncertainty during extreme flooding events (Laborde, 2018). Addressing the mounting challenges facing these peatlands and their communities will necessitate a hybrid conservation approach that integrates local ecological knowledge with scientifically informed environmental governance (Pascual et al., 2021; Rarai et al., 2022). Globally, conservation scientists are calling for research and policy development that is place-based, co-produced, and adaptive (Bennett et al., 2021; Kobluk et al., 2024; West et al., 2020), particularly in water-dominated systems like wetlands where system components are uniquely entangled and threatened (Birnie-Gauvin et al., 2023; Linton & Budds, 2014; Jenkins et al., forthcoming). Our work answers these calls and contributes to a growing body of literature on human-peatland interactions in the Congo Basin (Jenkins et al., this issue). It furthermore builds on existing work in conservation science to integrate social and natural science-based ways of knowing and valuing critical ecological landscapes (Hedblom et al., 2020). Ethnographic research on topics of scientific concern, thus, should be systematically integrated into research priorities, funding allocation, and policy development. Recognizing that the socio-cultural value of the Congo Basin's peatlands is tightly linked to and as spatio-temporally diverse as its fine-scale hydro-ecologies, we suggest that the "hydrosocial patch" be considered an essential unit (village-level) and method (transdisciplinary incorporating ethnography) of analysis for researchers seeking to produce data of relevance to policy and governance development.

Village	Reserve Locality	Political District	Research Team	Flooding Regime (during high-water season)	Adjacent Forest Type	Population Size	Dominant Ethnic Group
Bokatola	North	Epena	MB/CM	Fully flooded	Hardwood swamp forest	222	Nzobo (98%)
Mahounda	Center North	Epena	MB/CM	No flooding	Dry forest	252	Babolé (100%)
Itanga	Center	Epena	MB/CM	Partially flooded	Seasonally-Flooded Forest	343	Baitanga (90%)
Impongui	Center South	Epena	KM/TLN	No flooding	Dry Forest	155	Babolé (94%)
Edzama	South	Bouanela	KM/TLN	Partially flooded	Hardwood Swamp	425	Babolé (92%)
Likonda	South	Bouanela	KM/TLN	Partially flooded	Seasonally-Flooded Forest	373	Babolé (97%)

Table 1: Study village details: socio-ecological and research contexts ("Population Size" and "Dominant Ethnic Group" data derived from Bondeko, 2016).

Glossary of Bomitaba Terms			
Bomitaba Word	**French Equivelent**	**Meaning**	**Villages/Localities Where Term Was Heard**
Seasons		**Descriptions from Interviews**	
Muanga/Tamba Nfâ	Grande saison sèche	Big dry season: Typically falling between January and Avril	Muanga (All except...), Tamba Nfâ (Bokatola)
Mpela/Soba	Grande saison pluie	Big wet season: Typically falling between September and January	Mpela (All except...), Soba (Bokatola)
Ndjobolo/Essebo	Petite saison pluie	Small wet season: Typically falling between Avril and June	Ndjobolo (All except...), Essebo (Bokatola)
Essebo/Ekongo	Petite saison sèche	Small dry season: Typically falling between June and September	Essebo (All except...), Ekongo (Bokatola)
Types of Land and Water			
Ewassa	Foret Saisonnierement Innonde	"Example at the river when you get to the plain - forest where water enters easily;" "Where water enters;" "An open forest that floods (large compared to Moloukou);" "a terre firme (no mud) but water enters easily, like near the port;" "a seasonally-flooded area."	All
Mokolo		"To the North;" "An area that doesn't flood."	Meaning "an area that doesn't flood" in the South, otherwise meaning "to the North"
Eboungo	Vassiere	"A muddy area;" "A swamp"	All
Moloukou/Mobanda/Mololou:	Ruisseau	"Where you might go fish;" "Where you enter forest and go all the way to where there are fish;" "Places you go to put your nets;" "Open forest, often between two areas of terre firme;" "A seasonal passage for water;" "The route we use to access fields;" "In between two forests;" "The passage for water in the forest."	Moloukou (Likonda), Mobanda (Mohounda/Boha), Mololou (South)
Bonguta	Savane		All
Moungondo/Mokondo	Terre Firme	"Where it doesn't flood;" "Where we cut fields."	Mougondo (North), Mokondo (South)
Metele/Miyela		Stagnant water, a climactic anomaly during any season	Metele (Bokatola), Miyela (Itanga/Mohounda)
Dissawou	savane inondable	Flooded savanna	Mohounda
Mko		subteranean water that flows out of the forest through underground chanels into the main river system during the high-water season (August-December); Light-colored water that mixes with river water during flooding.	Mohounda

Table 2: Glossary of Relevant Bomitaba Words: Bomitaba terminology from interviews relevant to local hydro-climactic variables. This makes clear that there is not only a diversity in the types of water, land, and other environmental variables recognized by communities across the reserve, but also cultural (linguistic) diversity evidenced by the multiple village or locality-specific iterations of a single word. In word descriptions for "Ewassa" or "Moloukou," for example, it is also clear that local understandings of these types of land/water are linked to livelihood activities such as fishing and cutting manioc fields.

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Supplementary material - Chapter II

Study rationale: We conducted a systematic literature review in line with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) framework. Our review focuses on the responses of biodiversity in Congo Basin ecoregions to anthropogenic climate change, with a focus on the following questions: which type of responses to climate change observed in Congo Basin biodiversity? Which type of responses are projected? What are the literature foci in terms of biodiversity organizational levels and core ecological processes?

Table 1: The PICO (population, interest and context) framework used for this review

Population	Interest	Context
Congo Basin biodiversity at all organizational levels: - Organism - Population - Species - Community - Ecosystem	Predicted or observed responses to climate change	Peer-reviewed articles reporting documented or projected climate change impacts on biodiversity in at least one Congo Basin ecoregion (no time restriction)

Critical appraisal: Our systematic literature review only targets peer-reviewed literature, and selected studies have hence already undergone a thorough quality-control process. Data from gray literature was assessed by considering the level of details provided in the description of the methods, including data collection and analysis.

Article selection: Inclusion/exclusion criteria, including the decision tree for article selection, were discussed, refined and validated by all the authors, following a process including several search cycles. A first search performed in 2022 resulted in 2,109 records from both the Scopus and Web of Science databases. 2,098 records were screened by the first author, following the removal of duplicates. We excluded 1,914 records from the analysis: 1,004 based on the title and 722 by reading the abstract. Of the 184 publications selected for text screening, 156 were excluded as they did not match inclusion criteria (e.g. they did not include at least one Congo Basin ecoregion), 20 were excluded as they were not accessible, and 8 were excluded because they were conference abstracts. From the 34 gray literature reports initially retrieved, 12 studies matched the quality appraisal criteria and were considered for further analysis. In 2024, we performed a similar search on the platforms Web of Science and Scopus, which returned 550 papers. From those, we selected 65 papers by reading the title, and then 30 papers by abstract. Following text screening, 8 articles were finally added to the record list, bringing the final list to 104 included records (Figure 1).

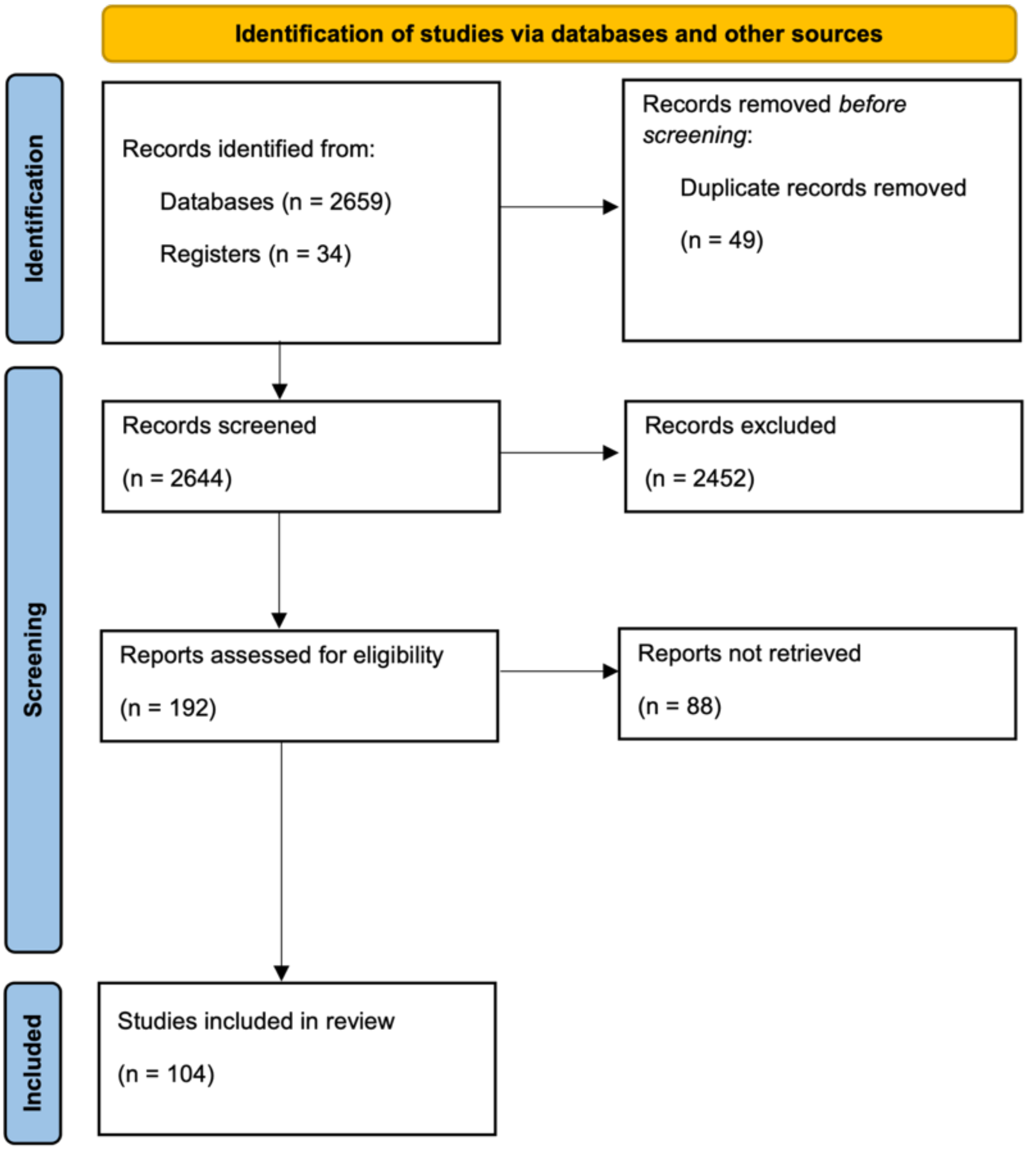

Figure 1: Flowchart outlining the different stages of the 2022 and 2024 literature search and review process, following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) framework.

Data collection and synthesis: Following an approach adapted from the frameworks established by Bellard et al. (2012) and Scheffers et al. (2016), we extracted information targeting following variables: bibliographic information (title, authors, publication year, journal), Congo Basin ecoregion, reported climate changes, other stressors considered, impacted biodiversity levels and ecological processes, type of impacts. One author was contacted to clarify an ambiguous paragraph. We synthetized primary results of each study and organized them by theme, according to each biodiversity level. We grouped selected studies per organizational level and ecological processes, in order to quantify knowledge gaps and knowledge clusters.

Limitations: This work was limited to peer-reviewed literature published in scientific journals in English. Although gray literature documents, in English or in French, were integrated to the review in order to alleviate knowledge gaps in the literature, further information may certainly exist at the local level. An expert-based literature identification (i.e. of non-published data, historical records or local reports), while beyond the scope of this study, could represent an accessible first step to complement the present work. Such an exercise should primarily target academic and local institutions from Congo Basin countries and should thus be conducted in French, widely used in the target region.

RCP and SSP scenarios: Representative Concentration Pathway (RCP) scenarios are four scenarios (RCP 2.6, RCP 4.5, RCP 6 and RCP 8.5) developed by the International Panel on Climate Change (IPCC) for its 2014 Fifth Assessment Report (AR5). They are linked with trajectories of greenhouse gas concentrations up to 2100. For the AR6, published in 2023, the IPCC developed Shared Socio-economic Pathways (SSP) scenarios, which are scenarios of possible socio-economic global changes (e.g. SSP1 on Sustainability or SSP5 on Fossil-fueled development).

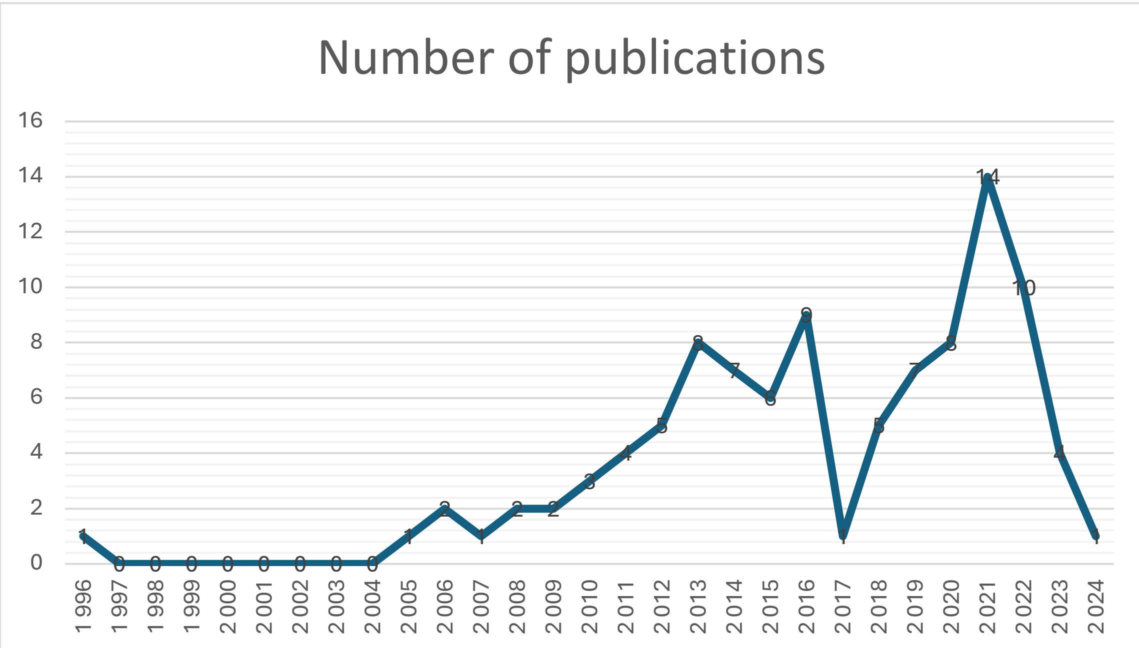

Figure 2: Number of published studies per year (until May 2024).

List of queries run on the Web of Science and Scopus databases:

Web of Science

TS=(("Congo Basin" OR "Central Africa" OR "tropical Africa" OR "Afrotropical region" OR "Guineo-Congolian forests" OR Cameroon OR Cameroun OR "Central African Republic" OR "Democratic Republic of Congo" OR DRC OR "DR Congo" OR Congo OR "Republic of the Congo" OR "Republic of Congo" OR Gabon OR "Equatorial Guinea") AND ("global warming" OR "climat* chang*" OR drought* OR cyclone* OR "CO2 concentration*" OR "extreme temperature*" OR "el Niño event*" OR "la Niña event*" OR "extreme weather event*" OR "climat* chang* impact*" OR "season* change") AND ("population reduction*" OR "population decline*" OR "increase in population size*" OR "range changes*" OR "range shift*" OR "range reduction*" OR turnover* OR "extinction risk*" OR "extinction probability*" OR survival* OR mortality* OR fertility* OR reproduction* OR ’’changes in phenology*" OR "advances in migration*" OR adaptation* OR "no change*" OR unchanged* OR "no effects*") AND (biodiversity OR rain forest OR wildlife OR species OR mammals* OR carnivores* OR herbivores* OR ungulates* OR primates* OR rodents* OR reptile* OR birds* OR fish* OR insect*))

Scopus

TITLE-ABS-KEY ("Congo Basin" OR "Central Africa" OR "tropical Africa" OR "Afrotropical region" OR "Guineo-Congolian forests" OR cameroon OR cameroun OR "Central African Republic" OR "Democratic Republic of Congo" OR drc OR "DR Congo" OR congo OR "Republic of the Congo" OR "Republic of Congo" OR gabon OR "Equatorial Guinea") AND ("global warming" OR "climat* chang*" OR drought* OR cyclone* OR "CO2 concentration*" OR "extreme temperature*" OR "el Niño event*" OR "la Niña event*" OR "extreme weather event*" OR "climat* chang* impact*" OR "season* change") AND ("population reduction*" OR "population decline*" OR "increase in population size*" OR "range changes*" OR "range shift*" OR "range reduction*" OR turnover* OR "extinction risk*" OR "extinction probability*" OR survival* OR mortality* OR fertility* OR reproduction* OR "changes in phenology*" OR "advances in migration*" OR adaptation* OR "no change*" OR unchanged* OR "no effects*") AND (biodiversity OR rain AND forest OR wildlife OR species OR mammals* OR carnivores* OR herbivores* OR ungulates* OR primates* OR rodents* OR reptile* OR birds* OR fish* OR insect*) AND (EXCLUDE (SUBJAREA , "NURS") OR EXCLUDE (SUBJAREA , "BUSI") OR EXCLUDE (SUBJAREA , "PHAR") OR EXCLUDE (SUBJAREA , "CENG") OR EXCLUDE (SUBJAREA , "MATH") OR EXCLUDE (SUBJAREA , "NEUR") OR EXCLUDE (SUBJAREA , "CHEM") OR EXCLUDE (SUBJAREA , "COMP") OR EXCLUDE (SUBJAREA , "ENGI") OR EXCLUDE (SUBJAREA , "ECON") OR EXCLUDE (SUBJAREA , "IMMU") OR EXCLUDE (SUBJAREA , "MEDI") OR EXCLUDE (SUBJAREA , "ENER"))

Additional search associated with the Amazon rainforest

Web of Science

TS=(("Amazon Basin" OR "Amazon" OR "Amazon rainforest" OR "Brazil" OR "Bolivia" OR "Peru" OR "Ecuador" OR "Colombia" OR "Venezuela" OR "Guyana" OR "Suriname") AND ("global warming" OR "climat* chang*" OR drought* OR cyclone* OR "CO2 concentration*" OR "extreme temperature*" OR "el Niño event*" OR "la Niña event*" OR "extreme weather event*" OR "climat* chang* impact*" OR "season* change") AND ("population reduction*" OR "population decline*" OR "increase in population size*" OR "range changes*" OR "range shift*" OR "range reduction*" OR turnover* OR "extinction risk*" OR "extinction probability*" OR survival* OR mortality* OR fertility* OR reproduction* OR ’’changes in phenology*" OR "advances in migration*" OR adaptation* OR "no change*" OR unchanged* OR "no effects*") AND (biodiversity OR rain forest OR wildlife OR species OR mammals* OR carnivores* OR herbivores* OR ungulates* OR primates* OR rodents* OR reptile* OR birds* OR fish* OR insect*))

Scopus

TITLE-ABS-KEY ("Amazon Basin" OR "Amazon" OR "Amazon rainforest" OR 'brazil OR bolivia OR peru OR ecuador OR colombia OR venezuela O

R guyana OR suriname) AND ("global warming" OR "climat* chang*" OR drought* OR cyclone* OR "CO2 concentration*" OR "extreme temperature*" OR "el Niño event*" OR "la Niña event*" OR "extreme weather event*" OR "climat* chang* impact*" OR "season* change") AND ("population reduction*" OR "population decline*" OR "increase in population size*" OR "range changes*" OR "range shift*" OR "range reduction*" OR turnover* OR "extinction risk*" OR "extinction probability*" OR survival* OR mortality* OR fertility* OR reproduction* OR "changes in phenology*" OR "advances in migration*" OR adaptation* OR "no change*" OR unchanged* OR "no effects*") AND (biodiversity OR rain forest OR wildlife OR species OR mammals* OR carnivores* OR herbivores* OR ungulates* OR primates* OR rodents* OR reptile* OR birds* OR fish* OR insect*)

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Supplementary material - Chapter III

Table 1: Number of local indicators and observations of changes reported by study participants (n=80), across systems and sub-systems.

System	**Sub-system**	**Number of indicators**	**Number of observations**				
			Village 1 (swamp forest)	**Village 2 (*terra firma* forest)**	**Village 3 (seasonally flooded forest)**	**Village 4 (*terra firma* forest)**	**Total**
Atmospheric system	**Temperature**	7	15	12	18	18	**63**
	Seasons	6	16	22	18	19	**75**
	Rainfall	8	17	10	20	19	**66**
	Fog	2	6	6	12	6	**30**
	Wind	2	12	8	16	14	**50**
	Total	**25**	**66**	**58**	**84**	**76**	**284**
Biophysical system	**River**	4	16	10	22	19	**67**
	Floods	14	77	45	85	107	**314**
	Soil	4	4	1	17	11	**33**
	Fire	6	19	14	21	15	**69**
	Forest	5	21	18	20	11	**70**

	Forest trees	46	16	35	36	34	**121**
	Fish	61	71	33	56	47	**207**
	Mammals	95	55	87	66	77	**284**
	Birds	50	20	31	19	28	**98**
	Non-timber forest products	10	23	54	20	21	**118**
	Total	**295**	**344**	**384**	**404**	**400**	**1531**
Human system	**Agriculture**	14	38	27	39	39	**143**
	Health	10	36	6	36	33	**111**
	Village trees	20	44	21	32	17	**114**
	Total	**44**	**125**	**70**	**119**	**93**	**407**
TOTAL		**364**	**554**	**537**	**618**	**585**	**2293**

Table 2: Indicators of change reported by respondents in the atmospheric system (n= 80 respondents), including respondent quotes.

Indicator of change	**Total number of citations**	**Quotes**
Increased temperature (in general)	30	*"Things have changed. I can't leave my house when it's hot. And yet I used to work in the sun. The sun is very uncomfortable* […] *when you stay in the sun, you get dizzy. I used to work in the fields under the sun."*
Increased temperature (long dry season)	10	*"The heat has increased, especially in the dry season* [mwanga]. *The heat even stings the nostrils when it's so hot. Every day, the children go straight to the water after school, even the adults go to cool off there […] even drinking is difficult, as the water in the wells heats up and looks like it's been heated. The water in the river is getting hot."*
Increased temperature (long rainy season)	6	*"We're in the rainy season* [pela] *and it's hot, everyone says 'oh, it's hot'. Normally, the really strong suns are in the dry season* [mwanga], *but now they're also in the rainy season* [pela], *because of climate change."*
Decreased temperature (in general)	5	*"It's cooler, because of the winds that come from the savanna. There are no longer trees to protect us and the wind blows into the village and breaks the trees."*
Unstable temperature (in general)	3	*"Now, in periods of heat, there is less stability, it can change by a week or a day."*
Increased rainfall (in general)	28	*"Generally speaking, there is more rain, and it is more frequent and more intense, especially this year."*
Increased rainfall (long rainy season)	6	*"The rains have exceeded. It rains without rest. In the rainy season* [pela], *it rains morning and night. It wasn't like that before."*
Reduced rainfall (in general)	5	*"Before, it used to rain all day in the rainy season* [pela], *from morning until 5pm, even flooding the plot, but now it doesn't rain like that* […] *anymore. The rains threaten, they come with wind, but they come with less intensity than before."*
Long rainy season in lieu of short rainy season	4	*"It's the first time that a short rainy season has caused people to flood, the calendar we had before has changed, it's the first time we've seen this* […] *there's upheaval even in our heads."*
Increased rainfall (long dry season)	2	*"There used to be no rain in in the dry season* [mwanga], *only from May onwards. The rains are more intense now than they used to be. Before, if there was heavy rain, it meant that the rainy season was starting. But now it rains as early as March."*

Unpredictable onset of rainfall	1	*"The rains have changed. Today there are rains that fall suddenly with no warning signs. Before there were signs in the sky like black clouds and thunder before the rains."*
Altered seasonal patterns	24	*"The calendar has been turned upside down. We no longer use the calendar. As soon as there's sun, we take advantage of it to burn the fields because there's a change in the rains." "We ask ourselves: is it the rainy season* [pela]*? Is it the dry season* [mwanga]*? It's hard to tell the seasons apart."*
Early onset of the long rainy season	24	*'The rains have changed. They used to start in August. This year, they started from March".*
Reduced length of long dry season	11	*"The dry season is becoming shorter, at least in recent years."*
Late onset of the long rainy season	8	*"In the past, at this time of year* [in October], *it would have rained, but now there's sunshine instead of rain, the water doesn't push anymore."*
Longer duration of long rainy season	6	*"Normally* […] *at the end of August, the long rainy season* [pela] *begins, lasting until September-October-November. This year, since June, is it* [pela]. *The water only recedes a little, then rises again."*
Longer duration of short dry season	2	*"Often, the dry season* [mwanga] *is extended, from December to July, instead of 6 months dry season. This creates major changes in society. Fish have the same problem: for them to circulate, they need water that corresponds to their body, otherwise they can't eat properly, they stay put, even if the bait is in front of them, they don't eat, they're not healthy. That's why sometimes there are no fish in the net or on the hook."*
Decreased fog (#days, length, intensity)	24	*"The fog is no longer intense. Before, for even a week you could see blurred. Now it's less intense. It's now down* [only] *at 5am, 6am. From 7am, you can see over the river. It only disappears for 5 days. It used to last for 2 weeks, all day long, the sunlight down* [would] *turn as white as the moon."*
Increased fog (#days, length, intensity)	6	*"You can see the fog when the water goes down* [at the end of the flooding season]. *It's much cooler now than it used to be."*
Increased frequency of violent wind (in general)	31	*"Some people flooded with their canoe while crossing* [the river]*, the winds pushed them out of the canoe, the waves came in and the cassava fell into the water crossing* […]. *The wind has been increasing like this for two years." "There is lot more wind because we've cut down too many trees. It's the trees that stop the wind."*

Decreased intensity wind (across seasons)	6	*"Some winds are intense, others not. Lately, the winds have not been so intense."*

Table 3: Indicators of change reported by respondents in the biophysical system (n= 80 respondent), including respondent quotes.

Indicator of change	**Total number of citations**	**Quotes**
Increased flood magnitude (in general)	56	*"The waters came after the dry season* [mwanga]*, it pushed on dry land really strongly, the trees near the river were flooded, there were even fish on dry land."*
Disrupted seasonality of floods in forests	5	*"The water is late in the forest, and the old man who spoke of the changing of the trimesters, without us believing him, was right."*
Increased floods in agricultural areas	30	*"Before, the fields would flood at the corners and a part would remain intact, but now it's the whole field that's flooded."*
Increased frequency of flooding events	45	*"This year, it is a total upheaval. There are possibly three floods for the first time. Before, there was not so much flooding, just in the corners. We can't move the village, where can we go?"*
Increased floods in village	55	*"In May, the villages were flooded* […] *all the villages in the North were flooded. They used dugout canoes in the village. People took refuge in the forest during the floods."*
Increased flood magnitude in forests	42	*"The water has pushed up a lot in the forest, it's made a mess of things. The water has* […] *at noon on 11 March. The water washed away our nets and hooks. At noon, I saw that the water had risen in 2 hours over 200 meters. I was at the ancestors' camp. It's a big river and I've never seen the water rise like that."*
Earlier onset of flooding events	26	*"This year, the flooding started in March. The floods used to arrive in August."*
Altered seasonal flooding regime	20	*"There's upheaval even in our heads. The real high-water season is now, but we can already see that the water is not going to rise much, there are too many variations."*
Accelerated rise in flood levels	10	*"There was a strong current and the water rose quickly in one day. I went back to the village to leave the child and the next day I went back into the forest, the water had already advanced a long way. We thought it was the end of the world, we were scared."*
Increased duration of flooding events	8	*"We are not used for the floods to be so long".*

Disappearance of flood patterns called "*miyela*"	4	"*Miyela* [referring to subtle shifts in water flow observed in the Likouala-aux-herbes river, traditionally signaling the onset of the short rainy season] *was in April; there are none now.*"
Late onset of flooding events	4	*"Things aren't as they used to be. At the moment, there should be plenty of water in the forest, but the young people who go fishing say that it's drying up."*
Reduced river depth (long dry season)	41	*"In the dry season, when the water goes down, it can be at the level of your calves or ankles because there is too much sand. Before there was depth, you could dive in completely."*
Increased river width (long rainy season)	15	*"In the rainy season* [pela], *again because of the disappearing trees, you can forget your way, the river has become very wide, you can end up in Epena by mistake."*
Increased river width (long dry season)	10	*"Before during the dry season* [mwanga], *the water dried completely. Now, it doesn't dry as well as it used to. It's bad because you don't find many fish. It's getting wider than it used to be on dry land."*
Increased erosion (riverbank or in village)	20	*"In* [my] *opinion, the soil is breaking up because it was under water, and with the heat, it dries out, breaks up and erosion progresses, causing the trees along the river to fall. The river becomes open, in front of the village and elsewhere."*
Increased occurrence of mud in village	6	*"The ground has really changed. Before, even after it rained, you could move around. There was no mud. Now, after a little rain, there's mud and the water stagnates in the village."*
Increased soil heat in village	6	*"The ground is very hot, even walking in the street is difficult, there are not many trees or fruits."*
Increased frequency of fire events	29	*"In the old days, the elders respected the seasons* […] *Now, very early on, around February or March, the savannas are burnt. When this happens, it creates disturbances and seasonal variations. Before, we used to wait until May to burn* […] *the timetable is no longer respected because of extreme poverty."*
Increased intensity (including length) of fire events Reduced occurrence of fire events	18	*"Now,* [we do] *a little fire, and it burns from the savanna to the forest. I realized it's because of the stronger sun. Even the trees with the green leaves burn."*
Increased occurrence of fire events in forested areas	6	*"The new fishermen go into the camps and no longer clean up the debris before setting fire to it. Now they directly set fires in the forest."*

Table 4: Summary of the 15 most observed indicators of biodiversity change in Lac Télé Community Reserve (n= 80 respondents), including respondent quotes.

Indicator of change	Total number of citations	Quotes
Reduced abundance of fish	56	"*Some species of fish have disappeared or become rare. Forest fires are destroying their homes and breeding grounds, and fishing pressure is increasing*."
Reduced caterpillar abundance	41	*"The caterpillars didn't produce much this year. They came out on time but didn't last. There were only three days during which there were a lot of caterpillars: the other days they came out a little, 30 caterpillars, we call them bifinio which means premature. Normally, the period during which we harvest good quantities lasts 2 weeks."*
Disrupted mammal migration	36	*"When they see the water coming,* [animals] *go on dry land. During the first* [flood], *the biggest one, the animals reached the dry land."*
Decreased gallery forest area, replaced by savanna areas	33	*"Forests are burning down because there are more fires, there is too much sun and less rain in the dry season."*
Increased tree mortality	30	*"Every year, the trees fall. This year, it looked like a cut field. Even on 1 hectare, the big trees were falling on top of each other. Big and small trees fall. There was water up to your chest. The soil was weakened."*
Reduced mammal species abundance	28	*"There used to be a lot of animals. We used to kill seven to ten elephants with the spear* [*assegai*]. *When it rained, they would go and eat on the edge of the savanna,* [and] *we would come and surround them* [...]. *These days, nothing."*
Reduced abundance in birds	24	*"There was one type of bird which reproduced a lot in the savanna during* [pela]. *We caught them to eat them. We don't see them anymore. We used to see them all the time* [...]. *There were lots of them on the palm trees near the river. We used to hear them a lot."*
Decreased forest fruit production	23	*"Fruits are still producing, but less than before. When I was growing up, it wasn't like that."*
Disrupted bird migration	23	*"The marabout stock come in large numbers in March, in 2023, March was the rainy season [pela], they came, but left just afterwards. They eat in groups, the water has to go down, they eat all types of fish in the ponds."*
Reduced abundance in *Gnetum africanum*	20	*"We used to find them in the fields, behind the houses, but now we don't find them as much as before"; "they were burned by the fire."*
Fish found dead	19	*"Fish like it cool. A lot of fish has died this year because of the heat."*
Reduced habitat for fish	17	*"The fish have moved because the water is not deep enough, the river is silted up."; "Their house was burnt*

		down by the fires."
Disrupted fish migration	15	*"The* [flood] *took the fish to the forest and brought them back to the savanna. Instead of leaving them to reproduce properly, they reproduced in disorder. Some moungoussou* (Parachanna obscurus) *started to reproduce in the forest, then came back to the savanna with the fry, then went back to the forest again, which upsets them." "Normally, the fish spawn in the forest ponds, then emerge into the river as the water rises. The floods in March took the juveniles out of the forest too soon; this year, it is a total disruption."*
Changed seasonality patterns for caterpillars	14	*"We observed that they appear with a slight delay of two weeks or even a month."*
Disappearance of fish species	14	*"There are many qualities of fish (mboto, souni, nina kombo….) which are no longer seen."*

Table 5: Climate change impacts on Lac Télé Community Reserve villages, % of respondents (n= 111). Not applicable indicates that the observation was not reported in the respective village.

System	**Impact**	**Village 1 (swamp forest)**	**Village 2 (*terra firma* forest)**	**Village 3 (seasonally inundated forest)**	**Village 4 (*terra firma* forest)**
Housing	Flooded houses	100%	Not applicable	43%	59%
Agriculture	Flooded agricultural fields	100%	13%	93%	86%
	Disturbance of seasonal activities	Not applicable	42%	87%	86%
	Smaller quantities of food	73%	83%	60%	21%
	Increase of human-wildlife conflicts	Not applicable	50%	17%	41%
	Increase cases of African cassava mosaic virus	Not applicable	58%	63%	52%

Fishing	Disrupted fishing season	57%	42%	53%	41%

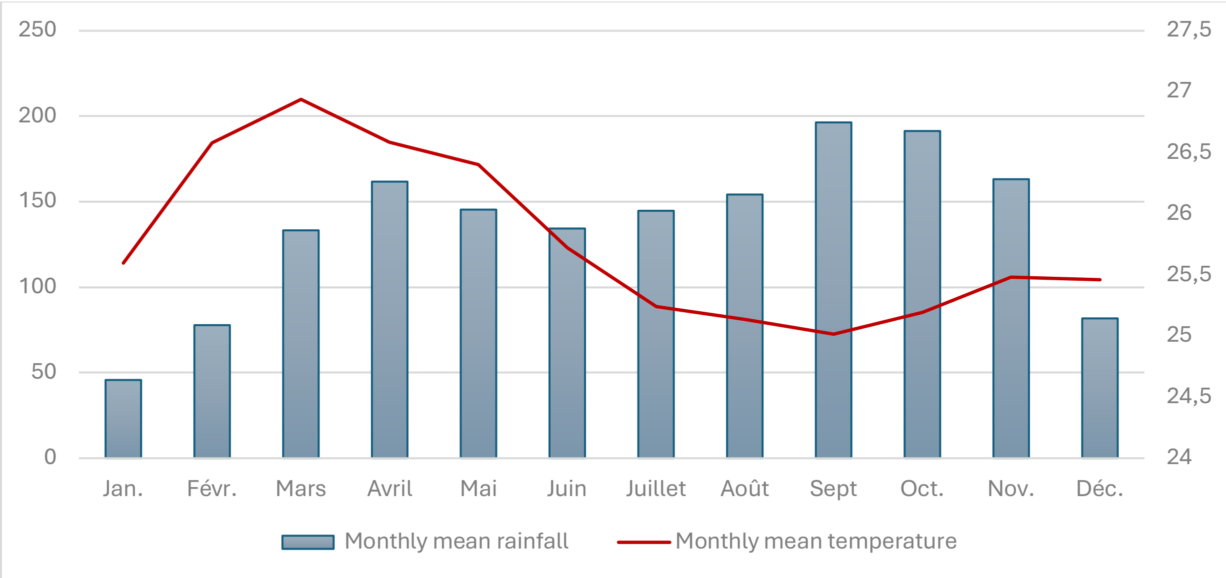

Figure 1: Seasonal variation in temperature and rainfall at the Impfondo meteorological station at the Impfondo airport. Data source: Agence Nationale de l'Aviation Civile du Congo.

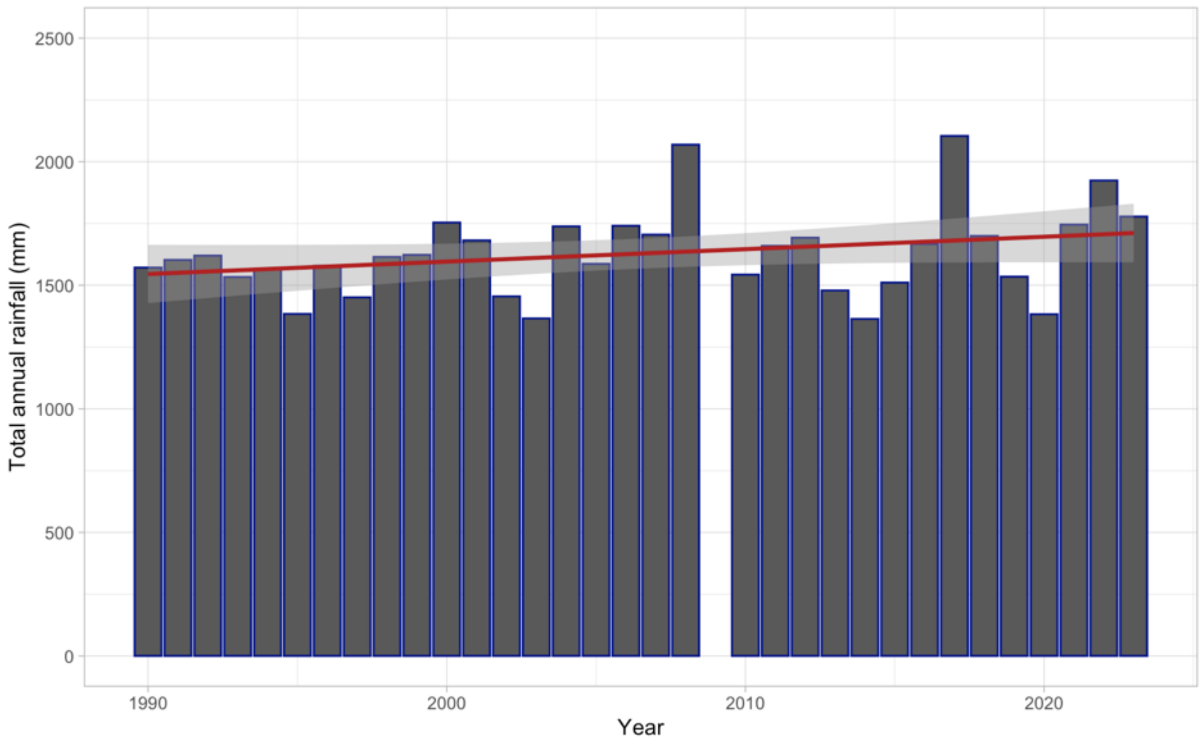

Figure 2: Total annual rainfall for the 1990-2023 period at the Impfondo airport. Data source : Agence Nationale de l'Aviation Civile du Congo.

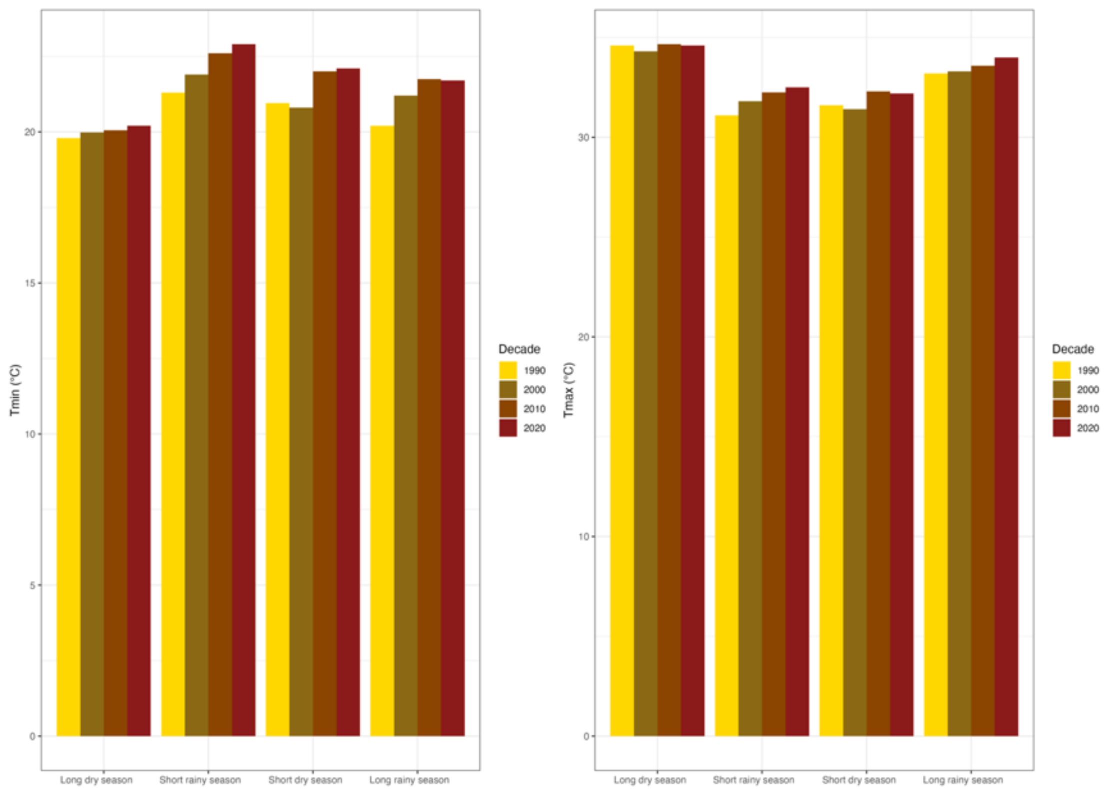

Figure 3: Seasonal minimum temperature (left) and seasonal maximum temperature (right) at the Impfondo airport. Data source : Agence Nationale de l'Aviation Civile du Congo.

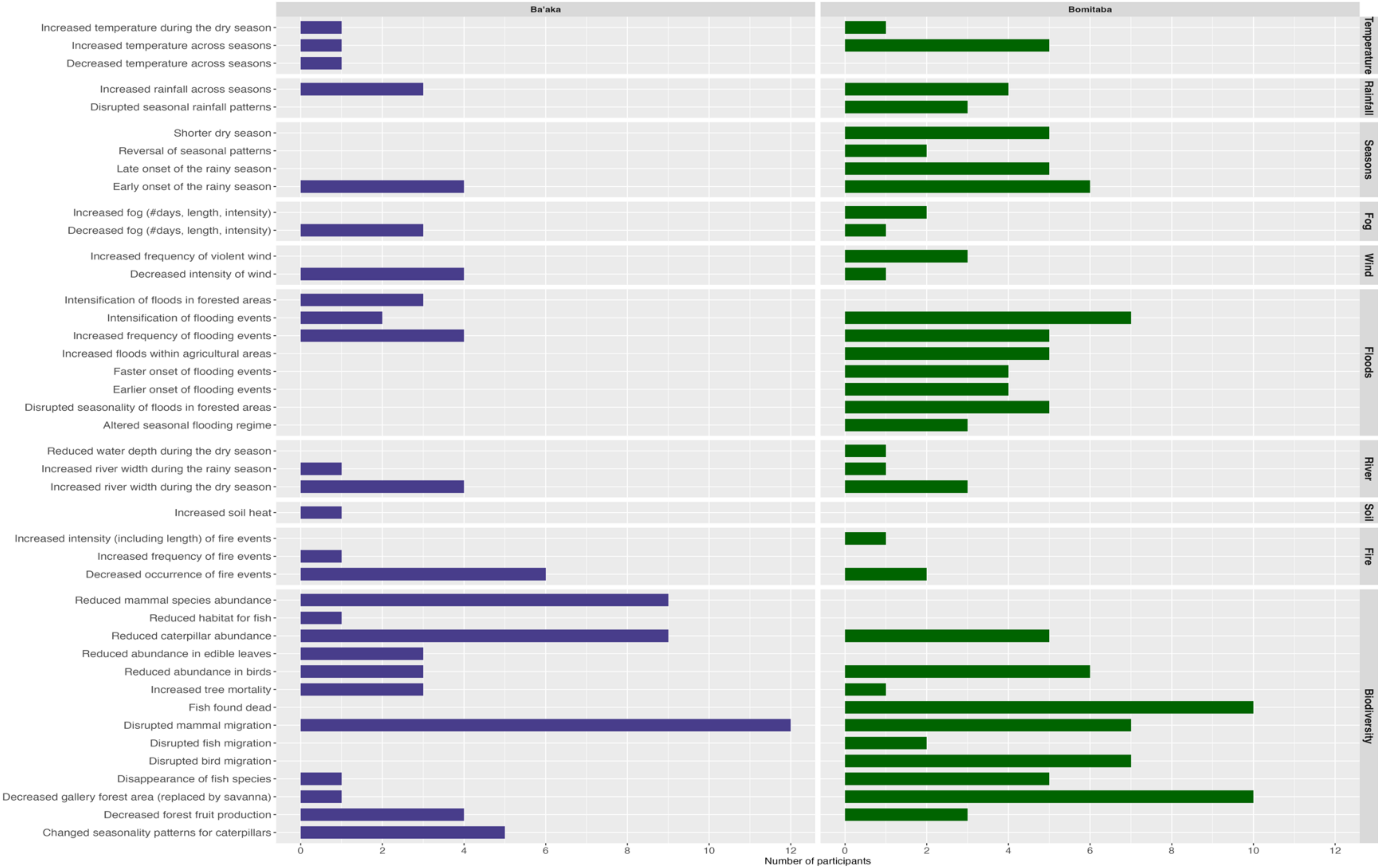

Figure 4: Indicators of change reported by Ba’Aka (n=11) and Bomitaba respondents (n=10). No significant difference between the groups (p = 0.152).

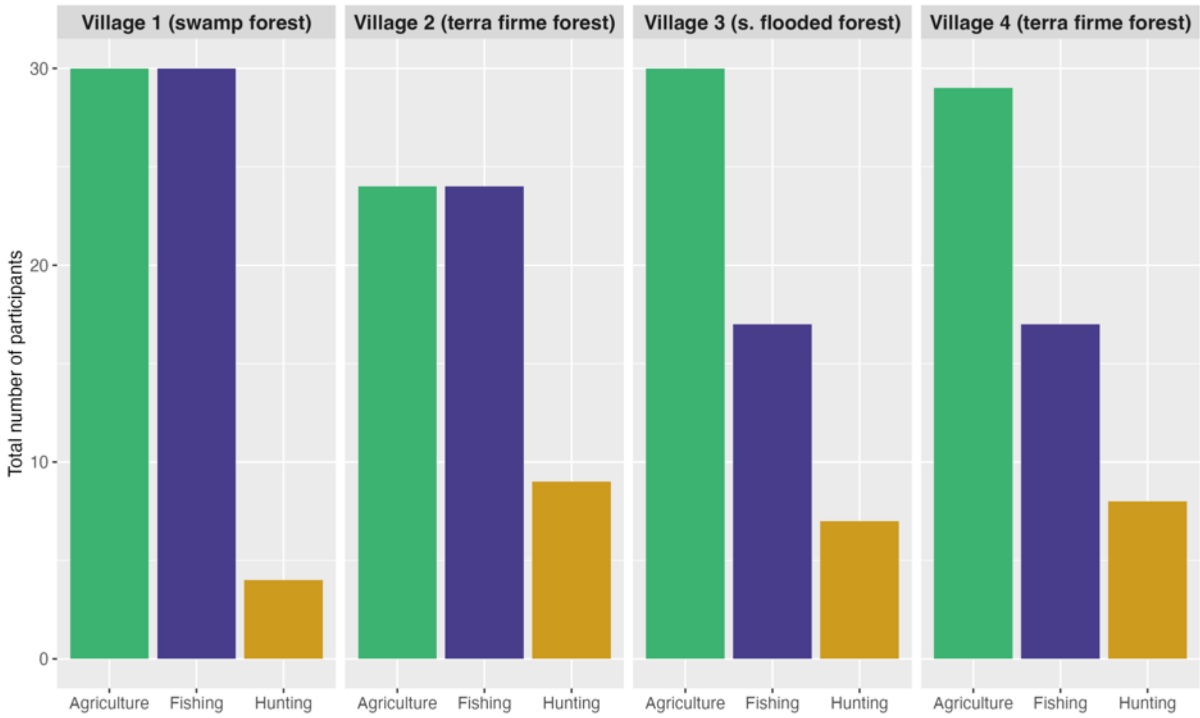

Figure 5: Primary subsistence activities in each village.

Guiding questionnaire used for exploratory focus group discussions:

<u>Seasonal calendar:</u>

Objective: Identify seasonal livelihoods and significant events (rainy seasons and dry seasons, holidays and festivals, agricultural activities including planting, harvesting, and marketing, hunting and fishing, periods of resource scarcity such as food, water, fish, or pastures, the calendar of climatic events such as storms, floods, droughts, and heatwaves).

Materials: Large sheets and colored pens or chalk in different colors.

- What are the main seasons? How do you recognize the change of seasons? What are the local names?

- What are the most important subsistence activities in the community? What are the local names?

- Details on planting: What are the main species cultivated? What techniques are used? In which season? When is the harvest? Where do you carry out these activities? Are there any people/groups of people who have more knowledge about this activity? What are the local names?
- Details on fishing: What are the main species fished? What techniques are used? At what time of the year? Were there times of the year when this activity was not done in the past? Has that changed? Where do you carry out these activities? Are there traditional fishing areas? Are these areas still respected? Are there people/groups of people who have more knowledge about this activity? What are the local names?

- Details on hunting: What are the main species hunted? What techniques are used? At what time of the year? Were there times of the year when this activity was not done in the past? Has that changed? Where do you carry out these activities? Are there traditional hunting areas? Are these areas still respected? Are there people/groups of people who have more knowledge about this activity? What are the local names?

- Details on collecting forest products: What are the main species collected most often? What techniques are used? At what time of the year? Were there times of the year when this activity was not done in the past? Has that changed? Where do you get the best forest products? Are there traditional collection areas? Are these areas still respected? Are there people/groups of people who have more knowledge about this activity? What are the local names? When do you usually get the best forest products?

- When are the major village festivals? What are the local names?

- Compared to when you were young, have there been any changes?

- If someone wants to know something about the forest (plants, animals, and specific areas), who among the villagers is able to explain it?

Historical timeline:

Objective: Establish the history of the village over the past 80-100 years. Relevant information includes: the date of the community's foundation/establishment; demographic changes, migration and settlement patterns; land rights over their territory and their evolution over time; trends in market interaction or changes in subsistence activities; approximate dates/periods when these events started to occur; extreme weather events; key infrastructure or social developments, including past disasters and changes in their nature, intensity, or configuration.

- How long has this village existed?
- Have there been any significant events?
- Has a road been built?
- Has a school been built?
- Has a new local chief arrived?
- Have there been any other significant events?
- Have there been any significant environmental events (e.g., extreme weather events)?

Guiding questionnaire used for the semi-structured interviews and the focus group discussions:

Part 1. Observed changes in climate, biophysical systems and drivers of change

1. Compared with when you were a young child, have the rains changed? (details on how they have changed, amount, duration, dry spells, showers, which seasons)
2. Compared with when you were a young child, has fog changed? (details on how it has changed, which seasons)
3. Compared with when you were a young child, has temperature changed? (details on how it has changed, which seasons)

4. Compared with when you were a young child, has wind changed? (details on how it has changed, which seasons)
5. Compared with when you were a young child, has frost changed? (details on how it has changed, which seasons)
6. Compared with when you were a young child, have hail storms changed? (details on how it has changed, which seasons)
7. Is there anything else you would like to add with regard to changes in local climate?
8. Why do you think the local climate has changed?
9. Compared with when you were a young child, has the environment here changed, e.g. floods, streamflow, landslides, soil erosion? (details on how it has changed)
10. Is there anything else you would like to add with regard to changes in your environment?

Part 2. Changes in the biological domain

11. Compared with when you were a young child, has the abundance of caterpillars, mushrooms or wild honey in the forest changed? (details on how it has changed)
12. Compared with when you were a young child, has the abundance of some trees or animals in the forest changed? (details on how it has changed)
13. Compared with when you were a young child, has the fruiting of some trees changed? (details on how it has changed)
14. Compared with when you were a young child, has the yield of some crops changed? (details on how it has changed)
15. Compared with when you were a young child, has domestic animals' health or number of offspring changed? (details on how it has changed)
16. Is there anything else you would like to add?

Part 3. Adaptive strategies used

17. Because of the changes in local climate you mentioned (e.g. less rainfall), and impacts on crops what have you changed? (details)
18. Was this change driven by a project from an NGO or the government?
19. Is there anything else you would like to add with regard to the things you have done to adapt to changes in climate and its impacts?
20. Is there anything else you would like to add?

Quantitative questionnaire used to assess adaptation strategies and livelihood change (adapted on site):

Sex:

Age group:

Main activities (farmer, fisherman, hunter, etc.):

Agriculture:

1. Are you still involved in agricultural activities? Yes/no/not applicable
2. Have you changed the location of your field? Yes/no/not applicable
3. Have you changed the size of your field? Yes/no/not applicable
4. Have you changed the distance of your field, compared to the village? Yes/no/not applicable
5. Have you changed the duration or frequency of daily agricultural activities? Yes/no/not applicable
6. Have you changed species grown? Yes/no/not applicable
7. Have you changed your agricultural techniques (e.g. cutting, seedlings…)? Yes/no/not applicable
8. Have you changed your soil conservation techniques? Yes/no/not applicable
9. Have you changed your use of fertilizers or pesticides? Yes/no/not applicable
10. Have you changed the amount of irrigation? Yes/no/not applicable
11. Do your fields produce as before? Yes/no/not applicable
12. Have you noticed any seasonal changes in relation to agricultural production? Yes/no/not applicable
13. Have you changed your livestock activities (e.g. more or less cattle)? Yes/no/not applicable
14. Are there any other change related to your agricultural activities that you would like to mention? Yes/no/not applicable

15. Fishing:
16. Do you catch the same amount of fish as before? Yes/no/not applicable
17. Do you catch the same qualities/species of fish as before? Yes/no/not applicable
18. Do you use the same fishing method as before? Yes/no/not applicable
19. Do you catch more juveniles than before? Yes/no/not applicable
20. Do you fish in the same areas? Do you fish further or less far than before? Yes/no/not applicable
21. Do you fish more than before? Yes/no/not applicable
22. When you go fishing, do you fish longer than before? Yes/no/not applicable
23. Do you fish at the same time as before? Yes/no/not applicable
24. Do you fish deeper than before? Yes/no/not applicable
25. Do you fish in the same season as before? Yes/no/not applicable
26. Are there more fishermen than before? Yes/no/not applicable
27. Are there any other changes related to fishing that you would like to mention? Yes/no/not applicable

28. Hunting and forest product collect:
29. Do you hunt more than before? Yes/no/not applicable
30. Do you hunt other qualities/species than before? Yes/no/not applicable
31. Do you hunt the same amount of animals as before? Yes/no/not applicable
32. Do you hunt in the same areas as before (further away, less far)? Yes/no/not applicable
33. Do you use the same hunting method as before? Yes/no/not applicable
34. When you go hunting, do you hunt longer than before? Yes/no/not applicable

35. Do you hunt at the same time of the year as before? Yes/no/not applicable
36. Are you collecting more forest products than before (e.g. plant, resin, building or medicinal material)? Yes/no/not applicable
37. Are you collecting more firewood than before? Yes/no/not applicable
38. Are there any other changes related to hunting or collecting forest products than you would like to mention? Yes/no/not applicable

Supplementary material - Chapter IV

Table 1: Evaluation metrics (Area Under the Curve, AUC and True Skills Statistics, TSS) for ensemble models across Datasets 1 and 2, ranked from lowest to highest for each metric.

Dataset 1				**Dataset 2**			
Model	AUC	Model	TSS	Model	AUC	Model	TSS
13	0.878	13	0.6220	11	0.950	11	0.7728
12	0.896	3	0.6847	7	0.951	12	0.7797
15	0.899	12	0.6902	12	0.952	15	0.7819
11	0.905	8	0.7059	15	0.952	14	0.7845
8	0.910	6	0.7117	10	0.953	6	0.7852
3	0.914	15	0.7230	2	0.954	9	0.7916
6	0.918	11	0.7316	6	0.954	13	0.7943
10	0.923	14	0.7434	9	0.954	4	0.7961
14	0.925	1	0.7508	14	0.954	10	0.7967
7	0.926	7	0.7602	8	0.956	7	0.7974
1	0.928	10	0.7602	12	0.956	2	0.7984
5	0.930	2	0.7620	1	0.958	1	0.8000
4	0.932	5	0.7702	4	0.958	5	0.8012
9	0.933	4	0.7713	5	0.958	8	0.8053
2	0.935	9	0.8005	3	0.960	3	0.8069

Table 2: Results of the Variance Inflation Factor (VIF) analysis, using a threshold of 6 to assess multicollinearity among predictor variables.

Dataset 1		Dataset 2	
wc2.1_10m_bio_5	3.026646	wc2.1_10m_bio_15	5.168545
wc2.1_10m_bio_6	1.684225	wc2.1_10m_bio_16	1.334101
wc2.1_10m_bio_15	3.858197	wc2.1_10m_bio_17	2.631147
wc2.1_10m_bio_16	1.239925	wc2.1_10m_bio_5	3.115618
wc2.1_10m_bio_17	2.175969	wc2.1_10m_bio_6	1.859728

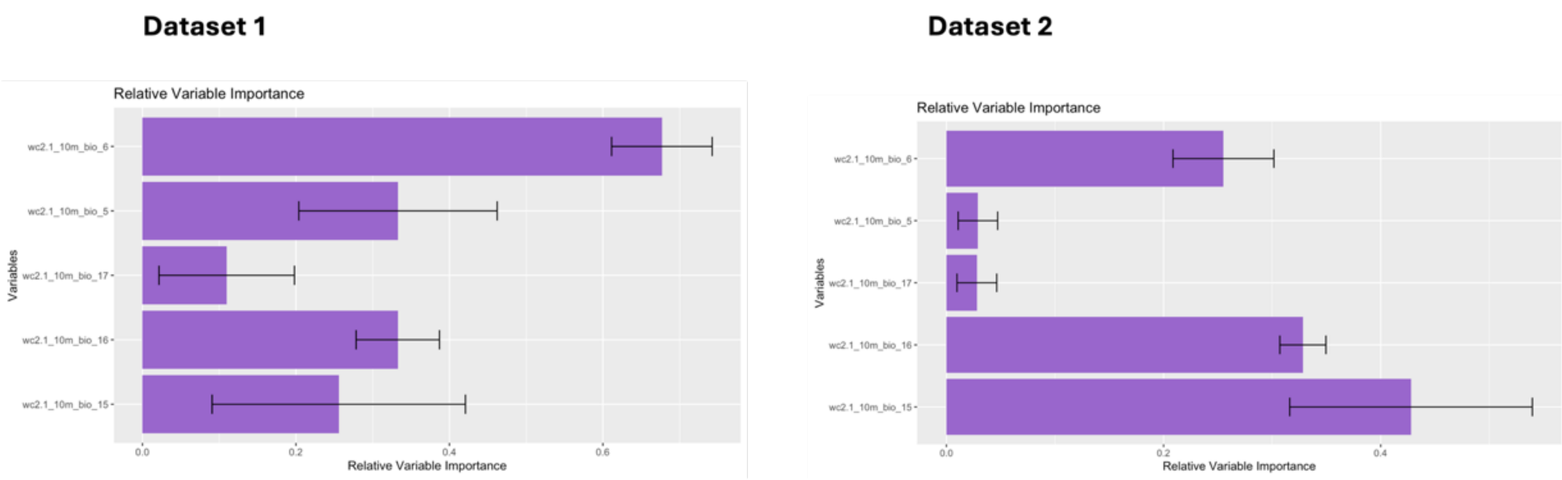

Figure 1: Summary of relative variable importance for Dataset 1 and Dataset 2, based on correlation metric.

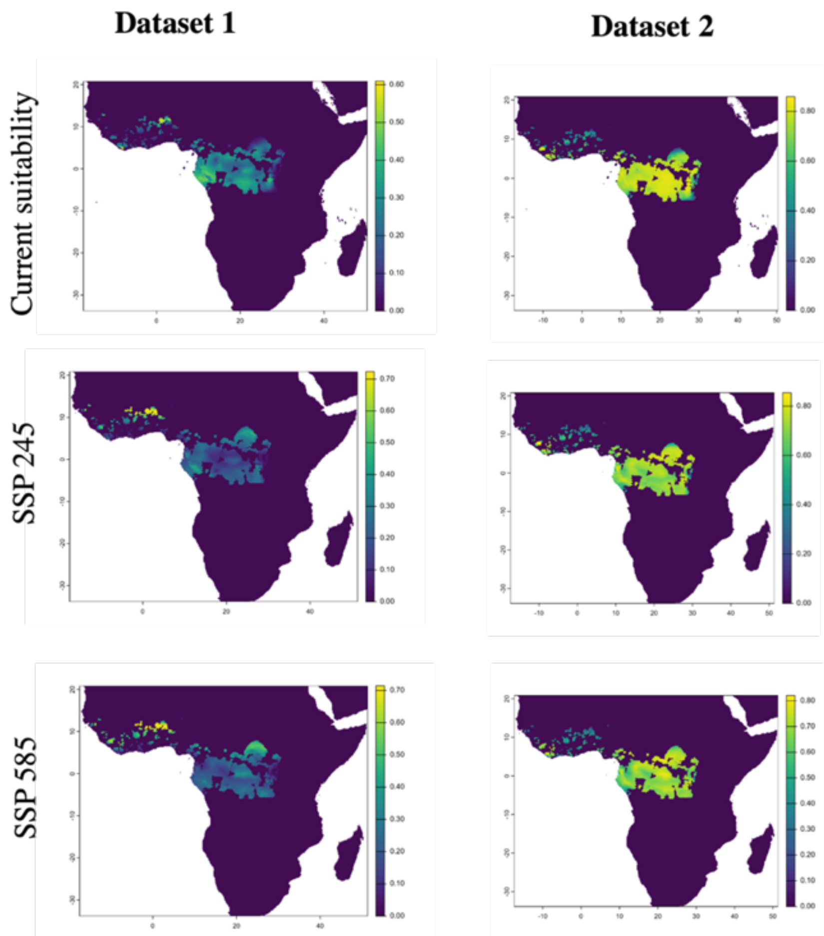

Figure 2: Ensemble continuous current and forecast climatic suitability within the current range of the forest elephant (forecast based on SSP 245 and SSP 585 scenarios). The two columns represent the two occurrence datasets (Dataset 1 and Dataset 2).

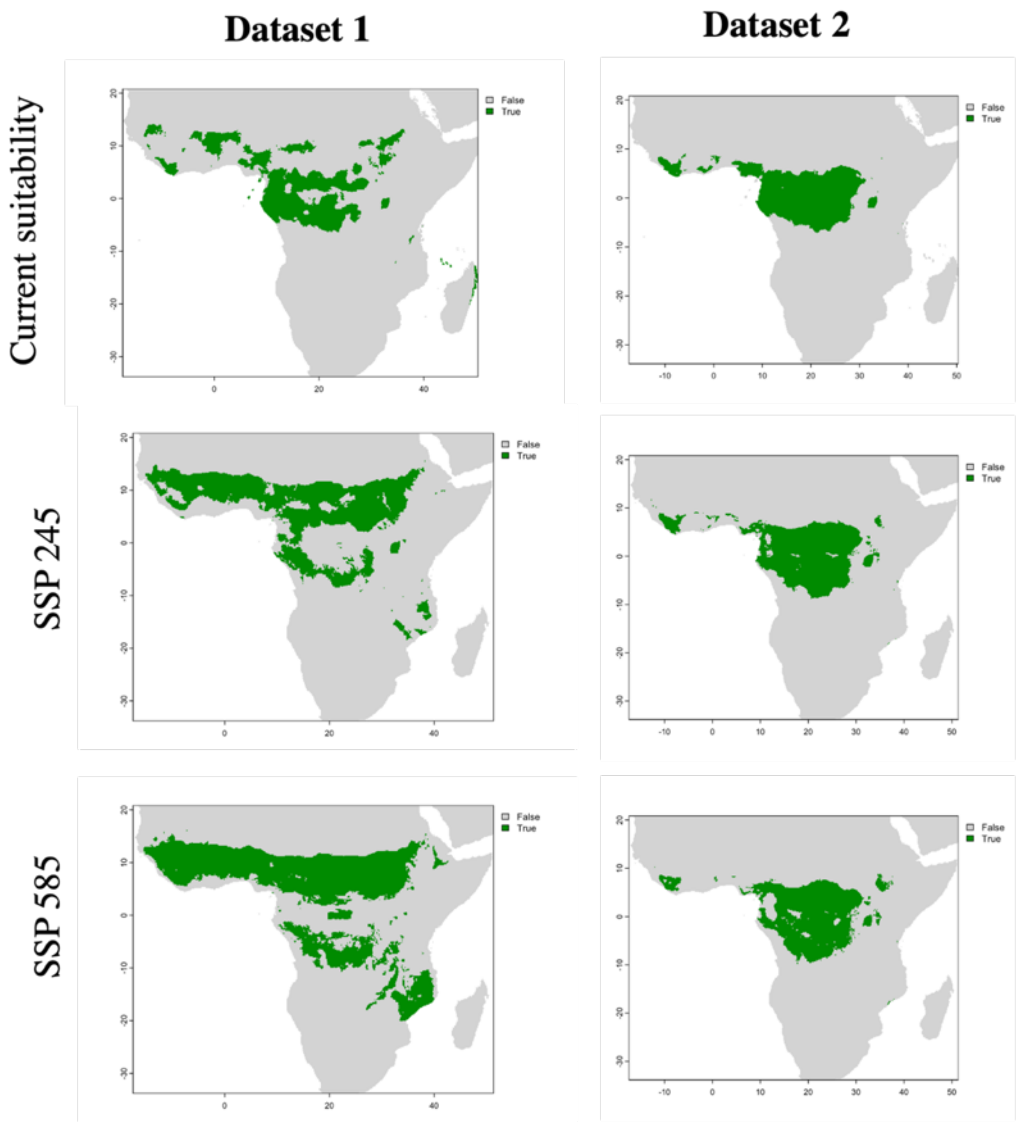

Figure 3: Ensemble binarized, non-range restricted, current and forecast climatic suitability for forest elephants (forecast based on SSP 245 and SSP 585 scenarios). The two columns represent the two occurrence datasets (Dataset 1 and Dataset 2).

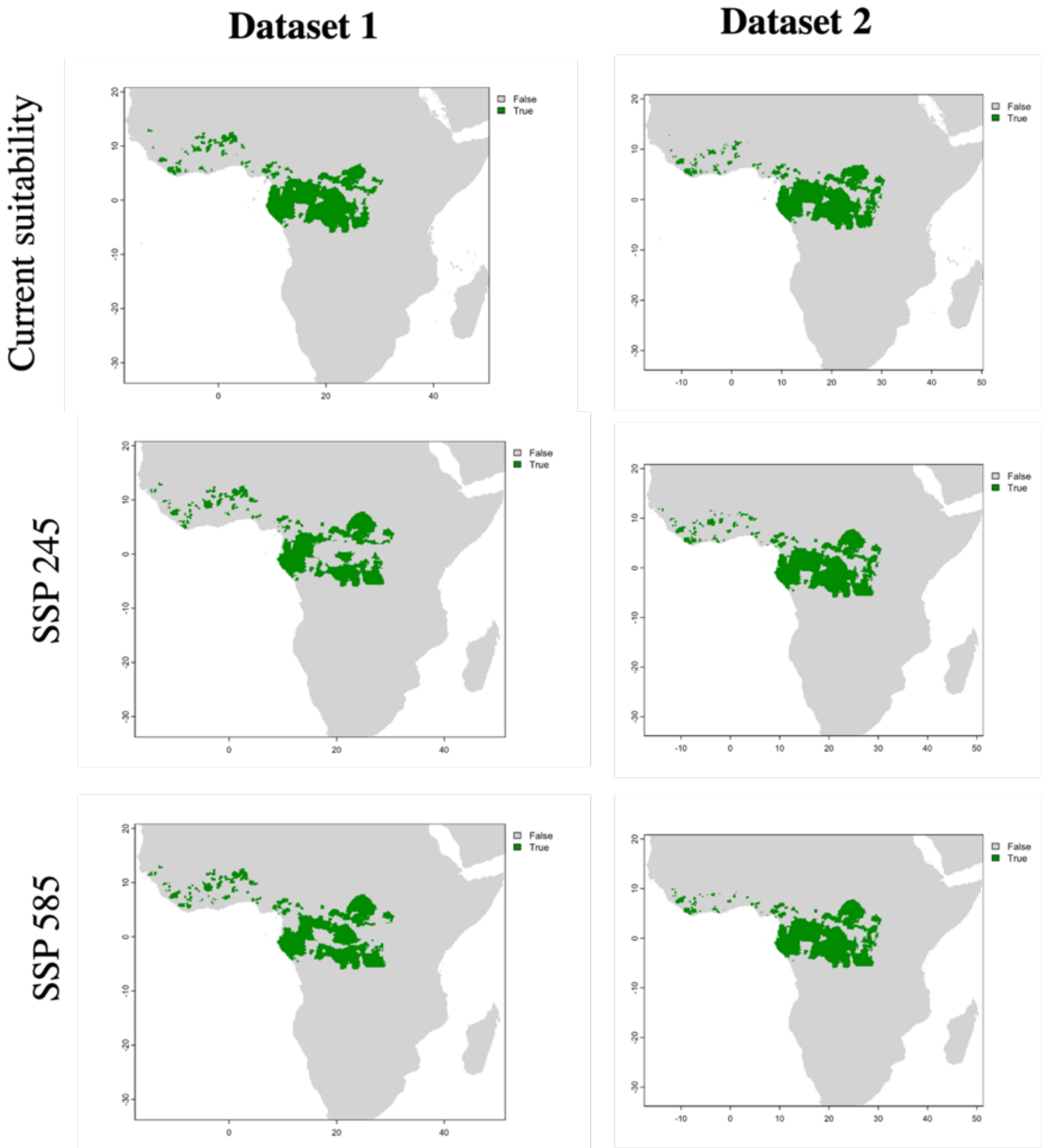

Figure 4: Ensemble binarized current and forecast climatic suitability within the current range of the forest elephant range (forecast based on SSP 245 and SSP 585 scenarios), applying a 5% binarization threshold. The two columns represent the two occurrence datasets (Dataset 1 and Dataset 2).

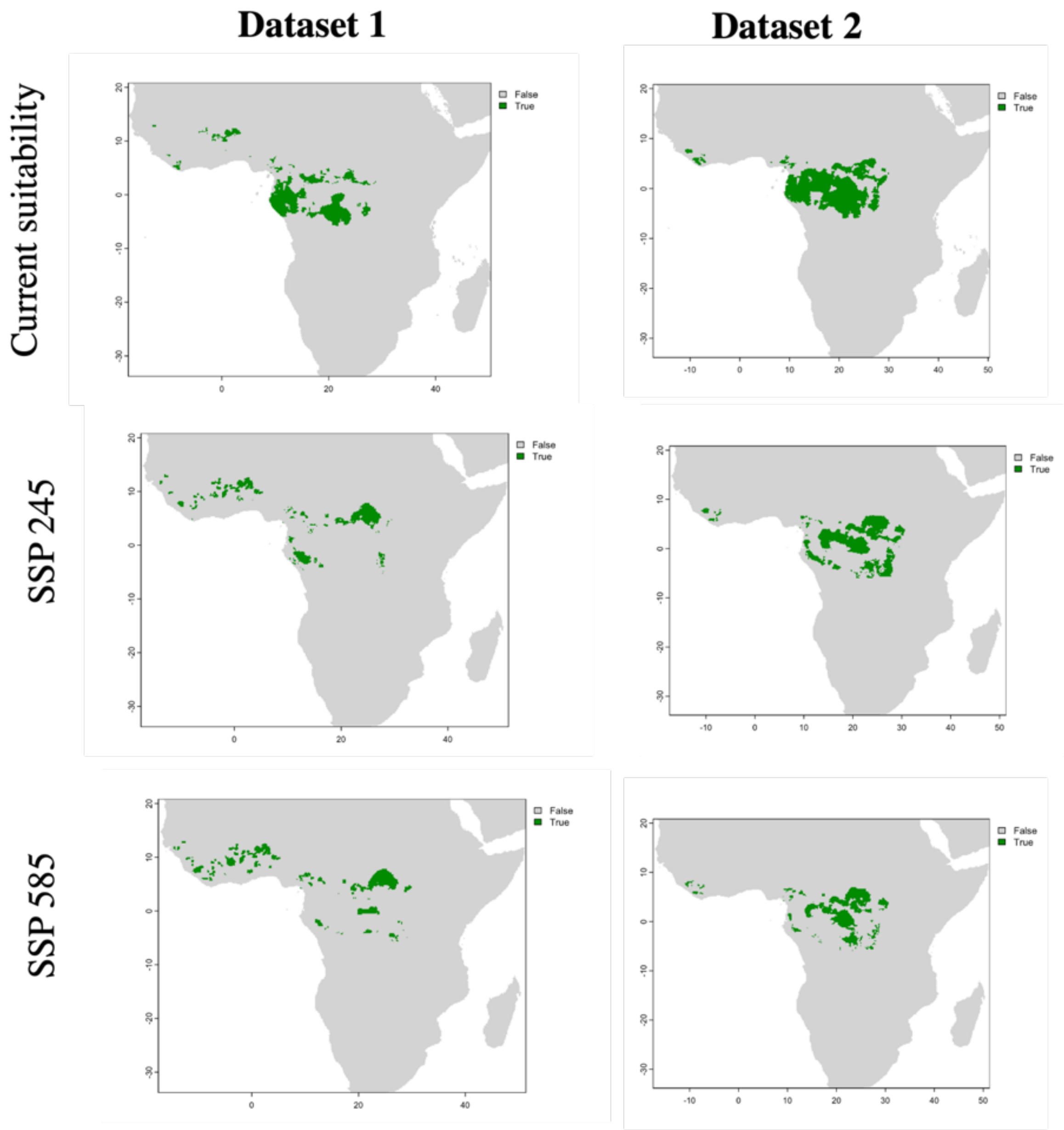

Figure 5: Ensemble binarized current and forecast climatic suitability within the current range of the forest elephant range (forecast based on SSP 245 and SSP 585 scenarios), applying a 15% binarization threshold. The two columns represent the two occurrence datasets (Dataset 1 and Dataset 2).

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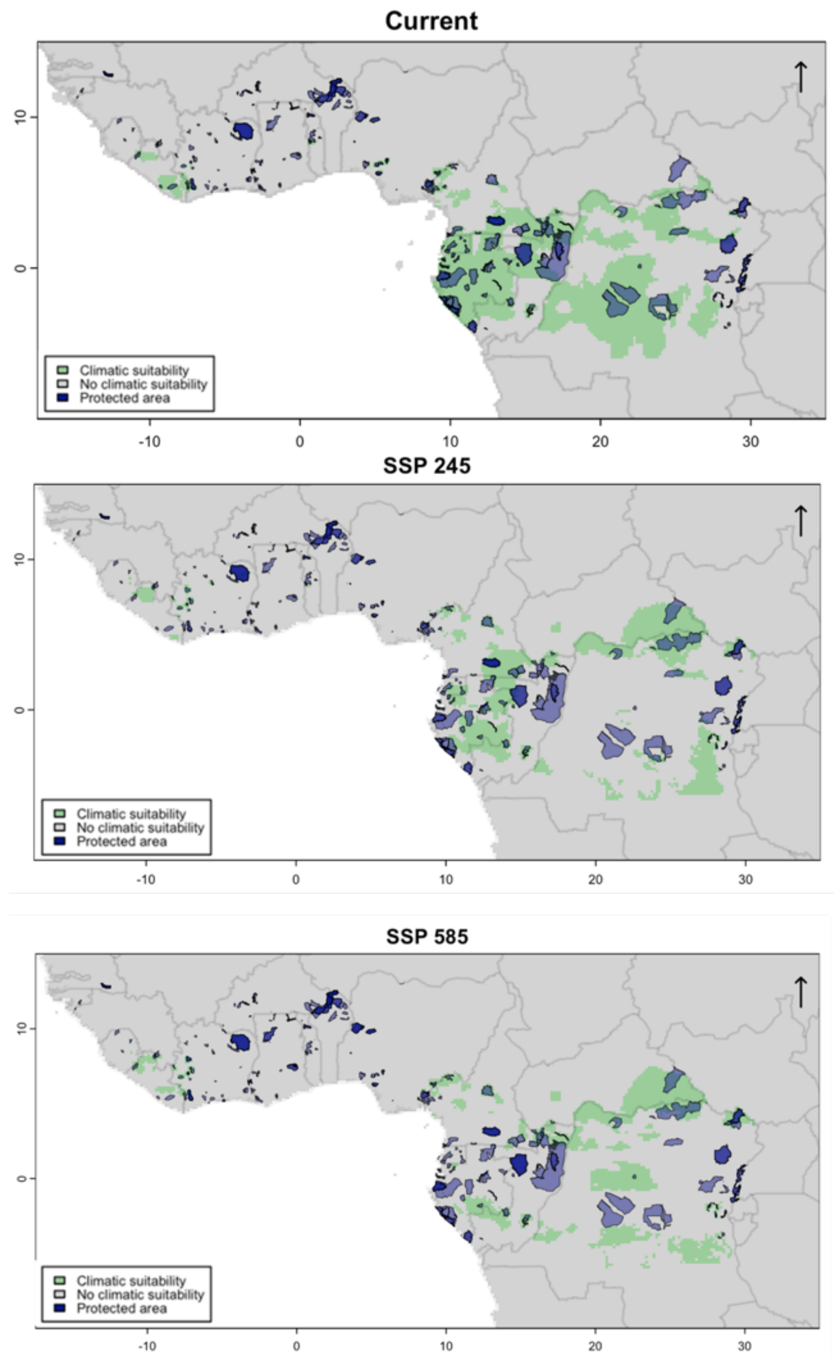

Figure 6: Consensus projections of climatic suitability within the forest elephant range across Dataset 1 and Dataset 2 (representing consensus in terms of current suitability, in SSP 245 and in SSP 585), in green, overlayed with current protected area coverage, in blue. Data source: World Database on Protected Areas.

Supplementary material - Response to the PhD dissertation evaluation

Reviewer 1

<u>Report</u>:

The PhD dissertation of Milena Beekmann is a multidisciplinary work that uses different geographical scales to investigate the direct and indirect effects of climate changes on biodiversity in the Congo Basin. This research work is particularly original for the field of studies on climate changes because of its multidimensional approach integrating data from ecology, geography, meteorology, ethnology and literature integrated with a modelling approach.

Overall, I really appreciated to read this dissertation. It is very well written, thus very enjoyable to read. Usually, in every PhD dissertation it is easy to find a missing space or some editing errors. I was impressed to see how here we hardly find any. The study design has been very well built and organized in the three main research studies. The aims of the whole research study are very clearly stated in the general introduction which is also a very comprehensive view of the state of art. I particularly appreciated the PhD candidate's synthesis skills which render the abstract, the general introduction and the general discussion very clear. They provide an effective overview of the study, an exercise that it is not always simple to achieve. I really loved that Milena provided the summary of the work in different languages including the main local language, Lingala. I believe the most difficult part for Milena Beekmann was to generalise and broaden the conclusions of her PhD research. The conclusions of the PhD being a bit too concise.

I congratulate Milena Beekmann for her impressive work both in the field and in compiling the vast amount of information included in her dissertation in addition to the data analyses and the innovative modelling approach used. This is commendable. This is a very original research combining different approaches to study the effect of climate changes not only at different scales but also on different study subjects including local human populations and their cultural changes and how they may affect biodiversity.

This study is thus adding rare information to a quite poor literature on effects of climate changes in the Congo Basin region both from the local human communities and wildlife point of view. I therefore think that the PhD research work of Milena Beekman is extremely high level of intellectual work. Herewith, I strongly recommend her research work as being suitable for the acceptance of the PhD defense and degree.

Some very minor changes are suggested.

<u>Response</u>: I express my gratitude to the thoughtful and constructive feedback provided by the Reviewer and their thorough evaluation of each chapter. I was very pleased to know that

the Reviewer considers that my research delivers rare data on effects of climate changes in the Congo Basin region both on wildlife and local human communities. I am encouraged by this review and will use it to further strengthen the scientific relevance of this work. I have proceeded to address the list of minor changes recommended.

Chapter II:

Comment: The author mentions in this chapter the plants of *Sarcophynium prionogonium* (Pag 45) et *Angylocalix oligophyllus* (p. 48). Both these plants are eaten by forest elephants because of their pith and fruit, respectively. In order to better link this chapter with the chapter IV (on the impact of climate changes on forest elephant future distribution), the author may want to mention this information also in chapter IV as a further example of a real impact on forest elephant diet.

Response: Many thanks for this very interesting comment. Mentioning the fact that *Sarcophynium prionogonium* (whose growth, fruit production and dispersal ability are impacted by climate change-driven increased aridity) and *Angylocalix oligophyllus* (for which a reduction in distributional range is predicted) are consumed by *Loxodonta cyclotis* will indeed be an interesting way to strengthen the link between Chapter II and Chapter IV. In Chapter IV, I have updated the "*Other relevant climate change impacts on L. cyclotis*" section on p.97, which now reads: "*For example,* Sacoglottis gabonensis*, an influential species in elephant movement and seed dispersal (White, 1994), exhibits rainfall-dependent fruiting patterns, suggesting that changes in precipitation could substantially affect its fruit production. Similarly,* Sarcophrynium prionogonium*, shows reduced growth, fruiting, and dispersal capacity under increasing aridity, while* Angylocalix oligophyllus *is projected to experience a contraction in its distributional range under future climate scenarios*".

Comment: P.46 Please specify "consider as staple food" for which species? Elephants? Gorillas?

Response: I agree that the species should be specified. I have updated the sentence, so that it now reads: "*Increased aridity is also found to affect the growth, also impacting fruit production and dispersal ability of* Sarcophrynium prionogonium *(Ley et al., 2018), a widespread perennial forest understory species from the Marantaceae family, considered a staple food for the western lowland gorilla (Magliocca & Gautier-Hion, 2002).*"

Chapter III

Comment: p. 63 "additional observations" please specify what additional observations have been made

Response: I have updated the sentence on p.62, which now reads: "*In all villages, additional contextual observations associated with reported climate change impacts on the local biophysical system or with adaptation strategies adopted by local communities were collected* *by M.B and C.M.M while accompanying study participants in daily subsistence activities (including farming, fishing, NTFP gathering and cooking)*."

Comment: How questions are asked is important and can affect the replies of local people. I think it is crucial to add in the supplementary information the list of all questions asked in the semi-structured interviews and in the questions asked during the quantitative survey.
In addition, the fact there have been different steps of language translations of the replies of the interviewed people may generate further confusions or loss of the original meaning. This should be somehow acknowledged in the limits of the study.
In addition, the author should better specify whether the interviews and the questions have been asked only orally or also through written documents? People may reply differently according to the method used. For instance, I believe the Ba'Aka did not know how to write therefore I believe they have been interviewed only orally and someone transcribed their reply somehow. For instance, Aka people may change drastically their answer in relation to how the question is asked and also just to please the asking person. All this makes very important to specify how the questions were asked and if orally for everybody or only for a subsample of people.

Response: Thank you very much for this detailed and important comment. I agree that a thorough description of the methods implemented in the Chapter III is crucial:

- Including the guiding questionnaires prepared for the semi-structured interviews and the quantitative survey is indeed of importance; both are already comprised in the Supplementary material (from p.188);

- I have included a sentence acknowledging that the use of translation between Lingala, Ba'Aka and French might have impacted the understanding of concepts communicated by study participants in the "*Study limitation*" section of the Chapter (p.64): "*We acknowledge that the necessary use of translation from Lingala to French, as well as from Ba'aka to French and French, may have influenced the transmission of concepts and nuances expressed by study participants*." I have also modified the "*Data collection*" section (p.62), in order to clarify the use of translation in village 2, which was indeed conducted directly from Ba'Aka to French, without an additional step: "*The Lingala language was used in most interviews and FDG, with occasional use of Bomitaba terms; responses were translated into French by C.M.M. In village 2, 19 interviews were conducted in Ba'aka, with the assistance of an additional interpreter who translated participant response from Ba'aka into French.";*

- I agree that it is important to specify the context of interviews, including the fact that they were conducted in a standardized fashion across the entire participant sample. Since all interviews were administered in an oral format, I included the sentence "*All interviews were conducted in an oral format.*" at the beginning of the "*Data collection*" section (p.62). Working with the Ba'aka translator, I ensured that all questions were linguistically clear while being phrased in a neutral manner to minimize interviewer bias and avoid influencing participants' responses to the extent possible.

Comment: P. 76 "Other adaptation measures, such as permanent emigration or having fewer children, were only considered in one village", please add which ones. It will be interesting to know this information.

Response: Considering the potentially sensitive nature of the data shared by study participant, I have opted to keep the study villages anonymous within this Chapter. However, I updated this sentence (p.75) to be more specific about the village in question, to the extent possible. It now reads "*Other adaptation measures, such as permanent emigration or having fewer children, were only considered in one of the most-flood affected village*".

Comment: P. 82 "We found that most adaptation strategies reported by respondents can be classified as "*possible risk or benefit*" for biodiversity", please provide the % to better define "most adaptation strategies".

Response: I updated the sentence according – see p.81: "*We found that 62.5% of adaptation strategies reported by respondents can be classified as "*possible risk or benefit*" for biodiversity, as their impacts are influenced by various factors.*".

Chapter IV

Comment: P. 90 **"**For Dataset 1, we implemented a target-group background sampling strategy, which aims at minimizing sampling biases by using the occurrences of taxa sharing similar traits within the study area (Barber et al., 2022)." I think this sentence deserves a bit more details. Even when reading the sentence that follows, it feels still that this method has not been well explained. I think that providing more information on how the selection was made etc.. will improve clarity.

Response: Thank you for highlighting this. I have improved the legibility of this sentence, so that the concept of target-group background and the selection of African megafaunal species is clearer. The sentence on p.89 now reads "*For Dataset 1, we applied a target-group background approach, which is considered a key strategy to address sampling bias in species occurrence records. This method leverages the combined occurrence data of ecologically similar taxa within the same region to approximate sampling effort for the focal species (Barber et al., 2022). The underlying assumption is that surveyors exhibit comparable biases when recording taxa with shared traits, thereby enabling a broader dataset to reflect general sampling intensity. Specifically, we used the COMBINE dataset (Soria et al., 2021) and included all African megafaunal species, defined as those with an adult body mass exceeding 40 kg (Malhi et al., 2016).*"

Comment: p. 97 While detailed information about the limitation of the study is typical of PhD dissertations, I would suggest to drastically reduced this part when finalizing it for publication.

Response: Thank you for this comment. I have reduced this section by 44% (down to 14 lines). It now reads as follows: "*Modeling species' responses to global environmental change inherently involves uncertainties (Araújo & New, 2007; Thuiller et al., 2019). We addressed some of these by implementing an ensemble modeling framework, accounting for variability across climate models and climate scenarios and focusing on a limited number of critical predictors. However, incomplete sampling of the species' range remains a significant limitation - particularly in Western and Central Africa, where indirect survey methods (e.g. road transects, dung counts and trail surveys) prevail (Thouless, 2016),. This is compounded by the logistical difficulties inherent in sampling vast, remote areas (De Boer et al., 2013), as by the scarcity of historical data and the pronounced human-driven contractions of the species' current distribution (Martínez-Freiría et al., 2016), potentially narrowing the breadth of climatic conditions assessed in projections under Dataset 1. To mitigate this potential bias and obtain a more comprehensive assessment of potential future climatic suitability, we compared estimates using Dataset 2. Despite these limitations, ensemble correlative models remain effective tools for assessing climate change impacts and informing conservation strategies under uncertainty.*".

Chapter V

Comment: In general, conclusion could be improved. Broadening the conclusions on how this work is adding crucial (and missing) information to understand actual and future effects of climate changes would certainly increase the value of this very interesting multidisciplinary research.

Response: Thank you for this feedback. Following this guidance, I strengthened the sections entitled "*Scientific and policy contributions*" (p. 107) and "*The Congo Basin in the Anthropocene: Concluding remarks*" (p. 110). I notably expanded on the novel knowledge generated through this thesis, from both a theoretical (including a systematic assessment of climate change impacts on biodiversity at the regional level, empirical evidence of direct and indirect climate change impacts on biodiversity in an under-researched site and projections of future climatic suitability for a keystone species, *Loxodonta cyclotis*) and a methodological perspective (including how to bridge local and regional-scale analyses, the role of local ecological knowledge in conservation science and the importance of interdisciplinary approaches in multifaceted climate change-driven ecological change). I also drew conclusions on key messages arising from this thesis in the context of other tropical ecosystems of importance, such as the Amazon rainforests.

Reviewer 2:

Report:

Appraisal of Individual Chapters - Introduction

The introductory chapter provides a comprehensive and conceptually robust foundation for the thesis. It clearly articulates the ecological and climatic significance of the Congo Basin while situating the research within the broader framework of the Anthropocene and global environmental change.

The candidate demonstrates a firm grasp of interdisciplinary research, effectively bridging biophysical science, conservation policy, and local ecological knowledge.

The writing is scholarly and well-referenced, establishing a clear rationale for the research objectives and methodological choices. While the density of the text may be challenging for some non-specialist readers, the depth of insight reflects a commendable command of complex literature. Integrating multiple disciplinary perspectives ensures relevance to a broad academic and policy-oriented audience. Including a conceptual diagram or summary table could enhance clarity and accessibility.

Strengths:

- Clear articulation of research aims and a multi-scalar framework
- Strong interdisciplinary positioning
- Deep contextualisation within both regional and global discourses

Recommendation:

Minor stylistic edits to improve transitions and reader navigation.

Chapter II: Systematic Review of Climate Change Impacts on Congo Basin Biodiversity

This chapter (published already) offers a rigorous and timely synthesis of the literature on climate change and biodiversity in the Congo Basin. It demonstrates a solid command of systematic review methodologies and highlights critical thematic and taxonomic research gaps. The candidate successfully identifies underexplored ecological processes, such as evolutionary adaptation and species interactions, and emphasises the scarcity of empirical studies in the region relative to other tropical systems.

The review lays the groundwork for the subsequent chapters and stands as a valuable contribution, with implications for regional research prioritisation and international collaboration. The methodological clarity and use of structured classification enhance replicability and transparency.

Strengths:

- Methodologically rigorous and thematically relevant
- Provides clear guidance for future research
- Effectively links regional evidence gaps to broader scientific narratives

Recommendation:

Consider the inclusion of a visual summary of research gaps for broader impact.

Chapter III: Local Perceptions and Adaptation in the Lac Télé Community Reserve

This chapter presents a compelling analysis of local ecological knowledge and adaptation in a little-documented ecosystem, Lac Télé in the Democratic Republic of Congo. The methodological design - combining meteorological data with semi-structured interviews and focus groups - demonstrates the candidate's capacity for field-based, participatory research. The analysis is systematic and contextually grounded, offering rare insight into climate change impacts on biodiversity from a community perspective.

Classifying adaptation strategies by their potential biodiversity impacts is especially valuable for informing policy and conservation planning. The study's robust sample size, rigorous triangulation methods, and ethnographic depth reflect a high standard of qualitative research.

Strengths:

- Groundbreaking documentation in an under-researched site
- Methodologically strong with cross-disciplinary relevance
- Highlights the significance of local knowledge for conservation planning

Recommendation:

In future work, incorporate visual tools (e.g., flowcharts or tables) to synthesise findings for non-specialist audiences.

Chapter IV: Climatic Suitability for Forest Elephants under Climate Change

This chapter delivers an empirically robust and methodologically innovative analysis of the climatic future of the African forest elephant (*Loxodonta cyclotis)*. The candidate applies a bioclimatic envelope modelling framework with ensemble forecasting, integrating two occurrence datasets to address spatial sampling limitations. The original approach strengthens the reliability of projections for a keystone species facing anthropogenic and climatic pressures.

Findings reveal that a substantial proportion of protected areas may lose climatic suitability by 2100, and that deforestation threatens the remaining suitable regions. The chapter offers critical policy implications, emphasising the need to revise protected area planning and explore integrative conservation strategies.

Strengths:

- Innovative use of dual dataset modelling to address uncertainty
- Substantial contribution to the climate vulnerability literature for tropical megafauna
- Direct conservation policy relevance

Recommendation:

Incorporating socio-ecological variables (e.g., human population density, infrastructure) into species distribution models could benefit future research.

Final Appraisal of the Thesis

This PhD thesis represents a significant and original contribution to climate change and biodiversity conservation, particularly relevant to tropical ecosystems and the Congo Basin.

The candidate has demonstrated a commendable ability to operate across disciplinary boundaries, skillfully integrating ecological modelling, literature synthesis, and field-based ethnographic research.

The multi-scalar approach - spanning regional systematic review, community-level inquiry, and species-specific modelling - provides a cohesive and comprehensive examination of climate change impacts. The research is conceptually innovative, methodologically sound, and practically relevant. Notably, the candidate addresses the ethical dimensions of conservation research, incorporating decolonial principles and emphasising local collaboration.

The thesis provides both theoretical insights and practical guidance for policy, especially regarding protected area planning, the role of local knowledge in conservation, and the need for climate-informed biodiversity strategies. Its policy contributions are well-aligned with global frameworks such as the Kunming-Montreal Global Biodiversity Framework and the UN SDGs.

Merits for the Award of the PhD Degree

Based on the originality, rigour, and interdisciplinary depth of the work presented, this thesis meets and exceeds the academic standards required for the award of the PhD degree. The candidate demonstrates:

- Mastery of relevant literature and theoretical frameworks
- Proficiency in diverse research methodologies (quantitative, qualitative, and spatial modelling)
- Capacity for critical reflection on methodological limitations and ethical considerations
- Substantive contributions to knowledge with clear implications for science, policy, and practice

Recommendation:

The thesis is of a publishable standard (as demonstrated already in a few chapters). The remaining unpublished chapters should be considered for academic dissemination in leading journals focused on conservation biology, climate change, and tropical ecology.

Response: I thank the Reviewer for their appreciative comments and overly positive feedback. I appreciate the recognition of the interdisciplinary scope and methodological rigor of my work, as well as the encouragement to disseminate the unpublished chapters. The recommendations are well noted:

- I have reviewed the thesis to ensure that it is free of typographical errors and to improve overall readability;

- I agree that the inclusion of visual tools enhances clarity and accessibility. While Chapter II is already published, I will consider it in future work. Similarly, a visual summary of findings is already incorporated into Chapter III (Figure 9, p.78);

- While the current Chapter IV focuses on climatic predictors, I agree that incorporating further socio-ecological variables would be beneficial for future research. When reflecting on the choice of predictor variables for this study, I considered both the quality of occurrence records, including their low positional accuracy, which limited the choice of spatial resolution, and the availability of layers for the entire study region (see "Occurrence data" section, p.87). Considering those limitations, I opted to overlay the prediction outputs with already published deforestation maps, which reflect the interplay between a reduction in climatic space and other drivers of habitat contraction for *L. cyclotis*;

- Many thanks for the suggestion to focus on the publishing the outputs derived from this PhD dissertation. While the Chapter II is indeed already published in the journal *Biological conservation*, Chapter III is currently in review in *Ecology and Society*, and I intend to submit Chapter IV for consideration to the journal *Nature Communication*.