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Review

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

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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 adaptive 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.

1. 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 and Yohe, 2003). In addition to direct impact, climate change also has indirect impacts on biodiversity, via human adaptation measures 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 2,485,670 km^2 (Grid-Arendal, 2014), 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 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 (Justice et al., 2001; Dezfuli, 2011). 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 30,6 Gt 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 semi-deciduous 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 (Aalen et al., 2015). Charismatic, critically endangered Congo Basin megafauna include 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 local and

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indigenous communities relying on forest resources for their livelihoods, 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 (FAOSTAT, 2022). 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 and 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). 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 (Akkermans et al., 2014; Haensler et al., 2013; Abernethy et al., 2016). 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 (Maidment et al., 2015; Asefi-Najafabady and Saatchi, 2013). While certain studies showcase a long-term drying trend (i.e., Hua et al., 2016; Malhi and 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., 2020; 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 Northern 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 kilometres 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 also 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 for 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 types of responses are already observed, and which ones are projected in the future?

2. 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., 2020). 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 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 Appendix A 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

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, insect, 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

an initial review of the available literature, we opted to use only English keywords 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 (see Appendix A).

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 (see Fig. 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) (see Appendix A).

3. Results

The literature search on climate change impacts on biodiversity in the Congo Basin returned 2000 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 on 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 %) (Fig. 2). In contrast, few studies focused on climate change impacts on ecological processes at lower organizational levels. Species genetics or morphology has 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 modelling studies (58 %) rather than in situ observed responses (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 %).

3.1. 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

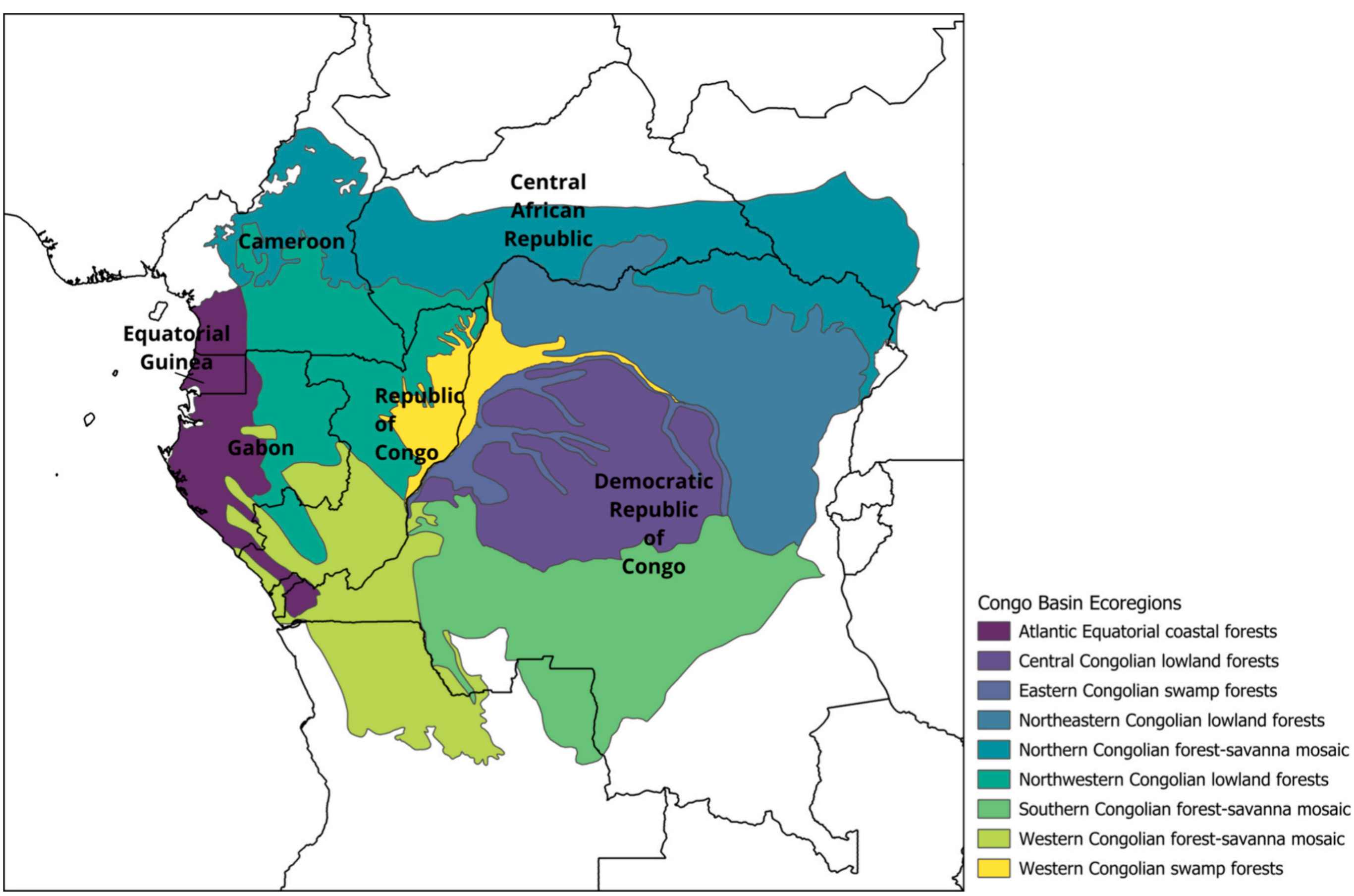

Fig. 1. Map of Congo Basin ecoregions.
(According to Olson et al., 2001).

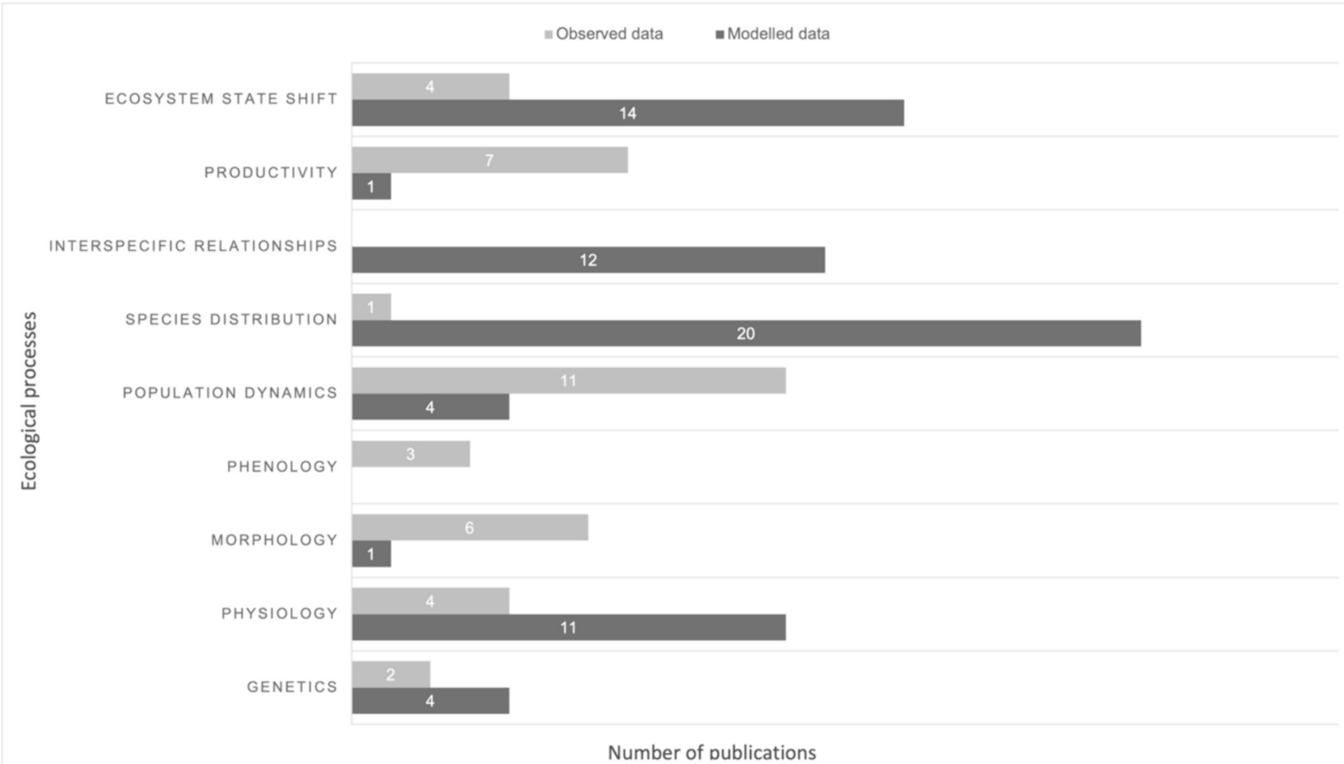

Fig. 2. Literature distribution in terms of studied ecological processes (n = 105 impacted processes).

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 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 Southwest Gabon, in the Cameroonian Sanaga River delta area and North of 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 group 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 Appendix A), 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 (Smith et al., 2021).

3.2. 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 modelling 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 with 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 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 3 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 to be a *Gorilla gorilla gorilla* staple food (Magliocca and 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 African forest elephants (*Loxondato* *cyclotis*) from 2008 to 2018 (Bush et al., 2020). 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.

3.3. Phenology

While phenological shifts have not been explored in ecological modelling, 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., 2020). 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 in Korstjens and 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. (2020) 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.

3.4. 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 Congo Kahuzi-Biega National Park (Batumike et al., 2022). 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 (Ockendon et al., 2012).

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.

3.5. 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 ranges 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. Modelling evidence indicates a northward range shift of about 3.45 km per year for the barn swallow (*Hirundo rustica*) population wintering over Western 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 (Şekercioğlu et al., 2012).

Among African regions, the Congo Basin is forecasted to experience the highest mammal species loss rate 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 (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 SSP5–8.5 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.

3.6. Interspecific relationships

We found evidence that distributional changes induced by climate change promote novel interspecific interactions in the Congo Basin. In the Central African Republic M'Baïki region, 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 the 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 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 the 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 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 invading 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 2-4.5 scenario, and additionally in the Northeastern and Southern Democratic Republic of Congo under SSP 5-8.5 (Lauer-Garcia et al., 2022).

3.7. 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 temperature trends (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.

3.8. Ecosystem state shift

Findings from both modelling 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 drought, 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 African 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 with 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 (Yu et al., 2014). 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 and 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 the Congo and Northern Republic of 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.

3.9. 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 amphibian 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).

3.10. 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 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.

4. 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 African 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., 2021b, or 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 with other African sites (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 modelling, field observations, experimental setups, 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 modelling or remote sensing outputs.

In 2021, Congo Basin Environmental Ministers emphasized the risks associated by 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 underresearched 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 (Stouffer et al., 2021; Moulatlet 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.

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CRediT authorship contribution statement

Milena Beekmann: Writing – original draft, Visualization, Supervision, Methodology, Data curation, Conceptualization. **Sandrine Gallois:** Writing – review & editing, Validation, Supervision. **Carlo Rondinini:** Writing – review & editing, Validation, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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