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Frugivore Declines Across Taxa Affect Forest Biomass

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ABSTRACT

Widespread disturbance to frugivory networks endangers ecosystem functioning. Carbon-rich tropical forests are particularly vulnerable to seed dispersal limitation from frugivore declines. However, understanding the ecological consequences of frugivore declines in tropical forests is challenging due to incomplete knowledge of existing frugivore-plant interaction networks. Here, we assessed the impact of frugivore loss on aboveground biomass (AGB) across 260 tropical forest plots in Gabon, using imputed interaction networks between 122 frugivore species and 99,349 individual trees. We investigated (1) how faunal degradation of frugivores affects AGB, (2) the relative importance of different vertebrate taxa to AGB maintenance, (3) the role of dietary redundancy and seed dispersal compensation in AGB change, and (4) geographic patterns in AGB change. Simulated degradation of endangered frugivores reduced AGB, but results varied by taxon: simulated degradation of elephants, apes, monkeys, ungulates, and bats decreased AGB, but degradation of carnivores and birds increased AGB. Results were sensitive to imputed interaction failing to account for unobserved interactions may underestimate future AGB storage. Results were also sensitive to compensatory effects: assuming seed dispersal compensation due to dietary redundancy dampened, and in some cases reversed, the magnitude of AGB change. Anthropogenic and environmental plot characteristics predicted vulnerability to AGB change. AGB loss tended to occur in forests at low latitudes, low elevation, low precipitation, and farther from villages. Primary forests were more vulnerable to AGB loss than secondary forests. Accounting for ecological interactions across broad taxonomic groups and spatial scales—not just charismatic taxa and in well-studied areas—is critical for understanding the nuanced effects of frugivore declines on ecosystem functioning.

1 | Introduction

Anthropogenic activities disrupt species interactions by reducing animal populations. Unsustainable anthropogenic pressures such as forest clear-cutting and hunting are driving faunal degradation, that is, a decline in animal populations from a community (Poulsen et al. 2023). In extreme cases, this leads to defaunation—complete functional depletion of animals from an area. By altering or weakening the relationships between animals and the species with which they interact, faunal

degradation threatens eco-evolutionary processes (Traveset et al. 2018; Bogoni et al. 2020; Tylanakis and Morris 2017; de Assis Bomfim et al. 2018). For example, mammal extinction and range contractions have decreased food web links by 53% globally (Fricke et al. 2022). Understanding the consequences of disturbed species interactions is necessary to predict how ecological communities may respond to declining animal populations.

By limiting seed dispersal, disruptions to species interactions can strongly affect ecosystem functioning and services. Seed dispersal

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regulates plant population dynamics (Barracough 2015), thereby influencing nutrient fluxes (Rogers et al. 2021), ecosystem processes (Dirzo et al. 2014), and landscape connectivity (Timóteo et al. 2018; Escribano-Avila et al. 2018). Altered plant community composition due to changes in seed dispersal can also change the functional composition of tree communities (Kurten et al. 2015), affecting ecosystem services such as resource provisioning, human health, and carbon storage (Harrison et al. 2013; Bello et al. 2015; Bogoni et al. 2020).

Faunal degradation can reduce forest carbon storage by decreasing frugivore abundances and limiting the dispersal of carbon-rich trees. For example, the loss of African forest elephants (*Loxodonta cyclotis*) has been shown to decrease carbon storage (Berzaghi et al. 2023). Large, hunted frugivores often, but not always (Harrison et al. 2013; Granados et al. 2018), disperse larger trees with higher wood density than nonhunted animals (Osuri and Sankaran 2016; Chanthorn et al. 2019). Consequently, over time, the loss of large-bodied frugivores can reduce average tree wood density and/or size, thus reducing the aboveground biomass (AGB) in tropical forests. The effects of faunal degradation on AGB are spatially variable due to heterogeneity in plant composition, dispersal distances, and spatial distributions of anthropogenic pressures (Osuri et al. 2016; Peres et al. 2016). In some cases, co-occurring frugivore species with overlapping diets can compensate for lost dispersal services (Sekar and Sukumar 2013; García et al. 2014). However, dietary overlap does not always confer compensatory effects; some disperser species play distinct functional roles in forest ecosystems (Dehling et al. 2016). Faunal degradation often leads to interaction deficits rather than compensation (Fricke et al. 2018; Reich et al. 2012), especially for endangered frugivores (Lamperty and Brosi 2022).

A number of challenges have limited our understanding of the effects of faunal degradation on AGB. One of these involves the incompleteness of ecological networks. Taxonomic, geographic, and methodological biases are common in seed dispersal studies (Escribano-Avila et al. 2018; Vitorino et al. 2022; Papadogeorgou et al. 2023) and result in incomplete networks. Imputing unobserved interactions by predicting “missing links” (unobserved interactions that nevertheless occur) can help increase completeness in ecological networks (Terry and Lewis 2020). Recent statistical advances jointly account for functional traits, phylogenetic relationships, taxonomic and geographic biases, and latent factors (unobserved variables inferred indirectly from models) to improve seed dispersal link prediction (Papadogeorgou et al. 2023). Subsequent work improves uncertainty propagation when species occurrences are unknown and studies suffer from extreme taxonomic bias (Kampe et al. 2025).

Here, we account for unobserved interactions and landscape-scale environmental variation to examine the consequences of faunal degradation on ecosystem functioning. We hypothesize that (1) faunal degradation of endangered frugivore species decreases AGB by reducing seed dispersal of large trees with high wood density; (2) degradation of large-bodied frugivores is more detrimental to AGB loss than degradation of smaller-bodied frugivores, as smaller-bodied frugivores are expected to consume only small-sized fruits whereas larger-bodied frugivores are expected to disperse a greater diversity of plants; (3) dietary redundancy across taxa mitigates AGB change; and (4) effects of faunal

degradation on AGB are spatially variable, and are more severe in primary compared to logged or secondary forests, as primary forests are expected to have higher baseline AGB. Large-scale, context-specific knowledge of the effects of faunal degradation on carbon storage is critical for advancing our understanding of the biodiversity crisis and its consequences for ecosystem functioning.

2 | Materials and Methods

2.1 | Study Area

We conducted this research using data from tropical forests across Gabon, where the ecological consequences of faunal degradation are prominent. Hunting in Central Africa reduces the abundance of large dispersers (Koerner et al. 2017; Beirne et al. 2019; Poulsen et al. 2017). By limiting seed dispersal, faunal degradation in Central Africa decreases recruitment of certain tree species (Rosin and Poulsen 2016), potentially decreasing AGB (Maicher et al. 2021) in some of the most carbon-dense forests in the world (Poulsen et al. 2020). However, Afrotropical frugivore network analyses are underrepresented in the literature, resulting in incomplete information regarding seed dispersal interactions (Escribano-Avila et al. 2018). Existing research on seed dispersal in Afrotropical forests has focused on large, charismatic, and easy-to-observe taxa. Large-bodied animals such as elephants and gorillas play key ecological roles in Central African forests (Poulsen et al. 2021; Haurez et al. 2018), but smaller-bodied, less-studied taxa such as duikers also disperse seeds (Dehaut et al. 2024).

Recently, researchers have accounted for biases and predicted unobserved interactions in Central African forests in a block modeling approach that identifies interactions at the group level (Durand-Bessart et al. 2023). Building on these advances, we conducted a species-level link prediction of frugivory interactions. Predicting interactions at the resolution of species, rather than broader taxonomic groups, enabled us to conduct a more nuanced assessment of the ecological consequences of faunal degradation. While the focus of the study is on Gabon, we used plant–frugivore interaction data across Afrotropical forests to inform our imputation of seed dispersal interactions.

Our faunal degradation analyses focused on the carbon-dense rainforests of Gabon in Central Africa. Gabon is home to many frugivores, such as the largest extant population of *L. cyclotis* and high duiker species diversity (Poulsen et al. 2017; Laguardia et al. 2021). Afrotropical forests also support a high diversity of frugivore interactions (Durand-Bessart et al. 2023). While Central African forests generally exhibit lower plant species diversity and stem density compared to other tropical regions, they support high tree AGB (Malhi et al. 2013). Gabon's forests, which cover the majority of the country's land area, are particularly carbon-dense and dominated by broad-leaf lowland rainforests (Poulsen et al. 2020).

2.2 | Data Collection

We used broad-scale data on binary, observed frugivore and plant interactions and species traits throughout Afrotropical forests from literature sources to improve link predictions, providing

a comprehensive understanding of potential interactions across the region. For the subsequent analyses, we used the availability of highly resolved, empirical botanical data throughout Gabon for simulating faunal degradation and capturing the effects of species interactions within Gabon's unique forest ecosystems.

2.2.1 | Observed Plant–Animal Interactions

We used binary, observed frugivory interactions from the Durand-Bessart et al. (2023) database, currently the most comprehensive available data on Afrotropical frugivory interactions. To update this database, we conducted a systematic literature search on Google Scholar (search details described in Supporting Information Additional Methods). We identified candidate papers by manually screening titles and abstracts for plant–animal interactions in Afrotropical forests. Among these, we screened for inclusion of frugivore dietary data, identifying 32 relevant papers that were not already included in the Durand-Bessart et al. (2023) database. We extracted interaction-level data including: (1) plant species, (2) frugivore species, (3) plant part consumed, and (4) interaction type (i.e., seed dispersal, seed predation, or herbivory; S2). We refined the database to only include interactions involving fruit and/or seed consumption by frugivores that were reported to the species level for both plants and animals and removed two nonnative conifer species. Although most interactions were mutualistic (primarily seed dispersal), some cases likely involved seed predation. Interactions represent both endozoochory (seed dispersal involving direct consumption by animals) and synzoochory (dispersal by seed-caching animals). The combined dataset, integrating our literature-derived database with the Durand-Bessart et al. (2023) database, included 10,635 interactions among 267 frugivore species and 958 plant species, compiled from 268 literature sources. Observations were collected across a range of forest types. Observations with limited focal taxa introduced taxonomic bias into the database: 82% of sources were animal-oriented, 6% of sources were plant-oriented, 10% were limited by both animal and plant species, and 1% were network studies of entire community of animals and plants.

2.2.2 | Frugivore and Plant Variables

To inform interaction imputations, we collected data on relevant traits from the literature for each frugivore species ($n=267$): log body mass (IUCN 2024; Jonathan Kingdon 2015), generation length (Pacifiçi et al. 2013; IUCN 2024), conservation status (IUCN 2024), habitat (forest or mixed) (IUCN 2024), and evolutionary history (Upham et al. 2019). Body mass and generation length reflect energy requirements, and conservation status and habitat relate to foraging preference and ability. Given that phylogenetically distinct frugivores tend to interact with different plant species (Pigot et al. 2016), we collected trait data at the species level when possible and to the genus level otherwise. We defined conservation status based on the International Union for the Conservation of Nature (IUCN) Red List. We obtained frugivore phylogenetic information using a consensus tree from VertLife (Upham et al. 2019). For plant traits relevant to frugivory, we collected wood density (Rejou-Mechain et al. 2017), fruit length, and fruit width (Durand-Bessart et al. 2023, S3). We obtained

plant phylogenetic data using V.PhylMaker (Jin and Qian 2019), which uses the angiosperm phylogeny generated from GenBank and Open Tree of Life data (Smith and Brown 2018).

2.2.3 | Botanical Plot Data

For botanical data, we used the National Resource Inventory of Gabon, which includes a semi-systematic sampling of 1-ha tree plots across the country (Poulsen et al. 2020). Field technicians from the National Parks Agency mapped, measured, and identified all trees ≥ 10 cm diameter at breast height (DBH; $n=99,349$) in 1-ha botanical plots ($n=260$) and collected associated metadata, including latitude, elevation, and exploitation status (primary, secondary, or logged). For detailed methodology, see Poulsen et al. (2020). We extracted precipitation (annual rainfall, mm) and temperature (mean annual temperature, °C) values for each plot from WorldClim using the R package raster (Hijmans et al. 2023). For each plot, we also calculated Euclidean distances to the nearest village and extracted elevation using the elevatr package (Hollister et al. 2023).

2.3 | Analytical Approach

We used probabilistic interaction imputations and simulation analyses to (1) determine how faunal degradation of endangered frugivore species affects AGB across Gabon, (2) detect the relative importance of seven frugivore groups (elephants, apes, monkeys, ungulates, bats, carnivores, and birds) to AGB maintenance, (3) evaluate the potential role of compensatory effects, and (4) analyze geographic patterns in AGB change caused by faunal degradation.

2.3.1 | Unobserved Interaction Imputation

To evaluate the sensitivity of simulation results to unobserved interactions, latent interactions were imputed by using Bayesian latent factor link prediction (Kampe et al. 2025; Papadogeorgou et al. 2023). Interactions were imputed across the African Frugivory dataset and subset to the flora and fauna present in the Gabon plots. The principal output of this model was a posterior network consisting of estimated interaction probabilities π_{ij} indicating the probability that frugivore i would consume the fruit of plant j given the opportunity, with $\pi_{ij} = 1$ for all pairs with known interactions.

For pairs without known interactions, interaction probabilities were estimated through the Bayesian Covariate Informed Link Prediction (COIL+) framework, relating latent factors—unobservable preferences and characteristics of frugivores and plants—to: (i) their propensity for interaction, (ii) their respective detection probabilities, and (iii) their observable traits. Sampling bias due to geographical and taxonomic limitations of the constituent studies was accounted for in the likelihood, which specified that observability of an interaction A_{ijs} between species i and j in study s was conditional on the existence of a true interaction L_{ij} , study focus F_{ijs} , co-occurrence of the species in the study region O_{ijs} , and latent species detection probabilities p_i and q_j :

$$P(A_{ijs} = 1 | L_{ij} = l, F_{ijs} = f, O_{ijs} = o) = \begin{cases} 0, & \text{if } lfo = 0 \\ p_i q_j, & \text{if } lfo = l, \end{cases}$$

where l, f, o were, respectively, binary indicators for the presence of a true interaction for the species pair, study focus on the pair, and co-occurrence of the species pair in the study of interest. We specified a phylogenetically structured prior covariance on the distribution of latent factors for both plants and frugivores to borrow information between related species, and determined the number of latent factors nonparametrically through a multiplicative gamma shrinkage process (Bhattacharya and Dunson 2011). All parameters were given Bayesian priors inducing semi-conjugacy, with posterior samples obtained via a Gibbs sampler. Further details on the method are provided in the [Supporting Information](#), with full specification and validation provided in Kampe et al. (2025).

We applied a cross-validation approach following Papadogeorgou et al. (2023), holding out 100 known interactions in each of 10 cross-validation replicates. We calculated *pseudoprecision* by taking the ratio of the mean posterior probability for held-out interactions to the overall mean posterior probability; we expect pseudoprecision to be in the range $(1, 1/\text{True interaction prevalence})$, with higher values generally indicating good discrimination of true interactions. Next, we calculated recall, defined as the proportion of held-out true interactions with a posterior probability > 0.5 .

2.3.2 | AGB Calculation

We estimated AGB of every individual tree using a pantropical model (Chave et al. 2014),

$$\text{AGB} = 0.0673 \times (\rho D^2 H)^{0.976},$$

where H was tree height, D was tree DBH, and ρ was wood density (Figure 1). For each tree, we determined the best taxonomic match of wood density using the R package BIOMASS (Rejou-Mechain et al. 2017), substituting mean dataset wood density when species, genus, or family level information were unavailable (16% of observations). In cases where tree heights were not directly measured, we built plot-level, diameter-height regression models (log1, log2, Weibull, and Michaelis functions) to predict heights based on DBH. Models were selected based on Akaike information criterion (AIC) values.

2.3.3 | Faunal Degradation Simulation

We stratified the binary, observed interaction network to only include frugivore ($n = 122$) and plant ($n = 495$) species that occur in Gabon, excluding rodents, which are known to be primarily seed predators. Based on interaction data and frugivore species range polygons (IUCN 2024; BirdLife International and Handbook of the Birds of the World 2020) of the frugivorous species in the dataset, we identified potential dispersers for every tree ($n = 99,349$) across the botanical plots. For the observed network, we considered a frugivore species a potential disperser of a given tree if that species had been documented dispersing a given tree species in our assembled literature database. We

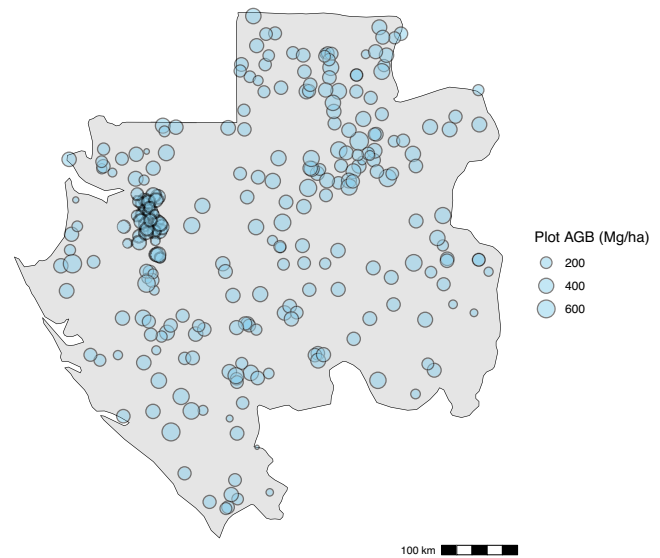


FIGURE 1 | Map of surveyed 1-ha forest plots ($n = 260$) across Gabon. Blue dots represent plots and their size varies relative to their initial (presimulation) AGB (Mg/ha).

conservatively excluded trees identified only at the genus or family level (35.6% of individuals) from association with dispersers due to unresolved taxonomic information.

First, we calculated the effects of endangered frugivore degradation on AGB in simulation scenarios using the imputed interaction network. We generated 100 simulated binary networks by drawing from the imputed posterior interaction probabilities. For each simulated network, we conducted 100 simulations under each of the three faunal degradation scenarios: 25%, 50%, and 100% recruitment limitation due to reduced seed dispersal. We conducted simulations under three scenarios by randomly replacing frugivore-dispersed trees with other trees in the plot. Replacement trees, therefore, were more likely to be not frugivore-dispersed. Specifically, we simulated faunal degradation of the five endangered frugivore species in our data, those which are categorized as Endangered or Critically Endangered by the IUCN: *Cercocebus torquatus*, *Gorilla gorilla*, *L. cyclotis*, *Pan troglodytes*, and *Psittacus erithacus*. For simplicity, we assumed a 1:1 recruitment response, although this ratio is likely not 1:1 in nature; for example, we assumed a simulated loss of 1% dispersal resulted in a 1% loss of recruitment. We then recalculated AGB for each plot and degradation scenario to assess AGB change. We conducted 100 simulation runs under each scenario to generate mean AGB change per plot and 95% confidence intervals. We also conducted these simulations using the observed network (results available in the [Supporting Information](#)).

To examine heterogeneity in the effects of faunal degradation of different taxa, we also conducted simulations considering the degradation of frugivore groups (elephants, apes, monkeys, ungulates, bats, carnivores, and birds), removing trees known or predicted to be dispersed by a species in the targeted group present in Gabon (Figure S2). Frugivore groups were composed of varying numbers of species (Figure S1).

To identify the primary drivers (tree wood density vs. diameter) of AGB change under faunal degradation, we conducted t -tests

comparing three stand variables—AGB, wood density, and diameter—between dispersed and undispersed trees in each plot. We evaluated differences in stand variables between dispersed and undispersed trees in the imputed network based on 100 draws from the posterior interaction probabilities.

2.3.4 | Dietary Redundancy

Faunal degradation of particular taxa may be especially influential for AGB storage if other taxa do not disperse the same tree species. We therefore investigated dietary redundancy among frugivore taxa. To assess dietary overlap (extent of shared plant species consumed among multiple frugivore species) and niche width (diversity of plant species used by a frugivore species), we calculated Schoener's niche overlap and Levin's niche breadth for all taxa using the R package *spaa* (Zhang 2016). We calculated niche width and dietary overlap for both the observed network and the 100 simulated networks that were drawn from the imputed posterior interaction probabilities.

Next, we explored potential compensatory effects by conducting simulations in which we assumed complete compensation given dietary redundancy, that is, one taxa with dietary overlap completely compensated for the seed dispersal services of the faunally degraded taxa *for the tree species shared in the diets of both taxa*. For example, in the ape degradation scenario with compensation, we removed trees dispersed only by gorillas or chimpanzees, but trees dispersed by gorillas or chimpanzees *and* another taxon (birds, carnivores, ungulates, bats, monkeys, and elephants) were retained. Simulations otherwise functioned the same as faunal degradation simulations described above. We conducted these simulations for the imputed network.

2.3.5 | Geospatial Relationships to AGB Change

We estimated patterns in natural and anthropogenic environmental variation in relation to predicted AGB change. We removed the variable temperature from the analysis due to collinearity (threshold 0.6). We then built linear models for endangered species degradation, with mean AGB loss as the dependent variable and standardized natural (latitude, elevation, and precipitation) and anthropogenic (distance to nearest village, distance to nearest road, and exploitation) characteristics as independent variables. We conducted model averaging across the set of best fitting models (i.e., those with the lowest AIC scores) for each taxon using the R package *MuMIn* (Bartoń 2023). Geospatial relationships for the imputed network were based on the AGB values predicted using the previous 100 draws in the defaunation simulations.

3 | Results

3.1 | Unobserved Interactions Imputation

Imputation of latent interaction probabilities substantially increased the prevalence of frugivory interaction, or the proportion of all possible frugivore–tree interaction pairs between 122 frugivore species and 260 plant species in Gabon that would

interact if the opportunity presented. Interactions increased from 7.7% based on direct observation to 12.1% likely interactions after imputation (Figure 2), where “likely interactions” were defined as those with a posterior mean interaction probability > 50%. In addition to the 2290 known frugivory interactions recorded between frugivore and plant species occurring in Gabon, we predicted 1337 unrecorded interactions at the species level, a 58% increase in species interactions. Taking these interactions at the individual tree level yielded 130,362 additional potential frugivory interactions between frugivore species and tree individuals in our dataset, a 17% increase from the observed interactions at the individual tree level. The increases in the tree fruit species consumed varied by frugivore taxa (Figure S2).

Restricting the posterior network to species in Gabon, we obtained a pseudoprecision ratio of 8.71, indicating strong model capability to identify true interactions. Our model achieved a recall of 0.75 for interactions involving Gabonese species, indicating a robust ability to recover true interactions even when they were not included in the training set.

3.2 | Faunal Degradation Simulation

Forest stands across Gabon exhibited a wide range of estimated AGB values, with a mean of 296 Mg/ha (SD = 108). Simulated endangered species faunal degradation indicated significant AGB reductions in forest stands across Gabon, especially in high degradation scenarios (Figure 3). When endangered species were 100% degraded (defaunation; worst-case scenario), AGB losses ranged from 1.76 to 2.45 Mg/ha in the observed network simulations and 1.53 to 2.08 Mg/ha in the imputed network simulations (Figure 3a). Faunal degradation resulted in loss of AGB because endangered species tended to disperse larger trees in both observed and imputed networks; on average, trees dispersed by endangered species had 9% greater AGB and 9% larger DBH compared to trees not dispersed by these species (Figure S3). Interestingly, trees spread by frugivores had a lower wood density (by 4%, on average).

Simulated defaunation of elephants, apes, monkeys, bats, and ungulates led to a decrease in AGB because these taxa tended to disperse trees with high AGB values (Figure S4, Tables S1, S2). In contrast, simulated defaunation of carnivores and birds resulted in increased AGB because these taxa predominantly disperse trees with lower AGB values (Table S3). All frugivore taxa dispersed trees with greater diameters but lower wood densities than nondispersed trees (Figures S1, S6 and Tables S4, S5). Further, simulated defaunation of each taxon led to significantly lower AGB in the imputed networks compared to the observed networks (Table S1). Imputed networks had more species recognized as frugivore-dispersed compared to observed networks (Figure 3).

3.3 | Dietary Redundancy

The seven taxa played different functional roles in the seed dispersal network, which influenced their effects on AGB maintenance. Apes exhibited high niche overlap with other nonflying taxa in both the observed and imputed networks (Figure 4).

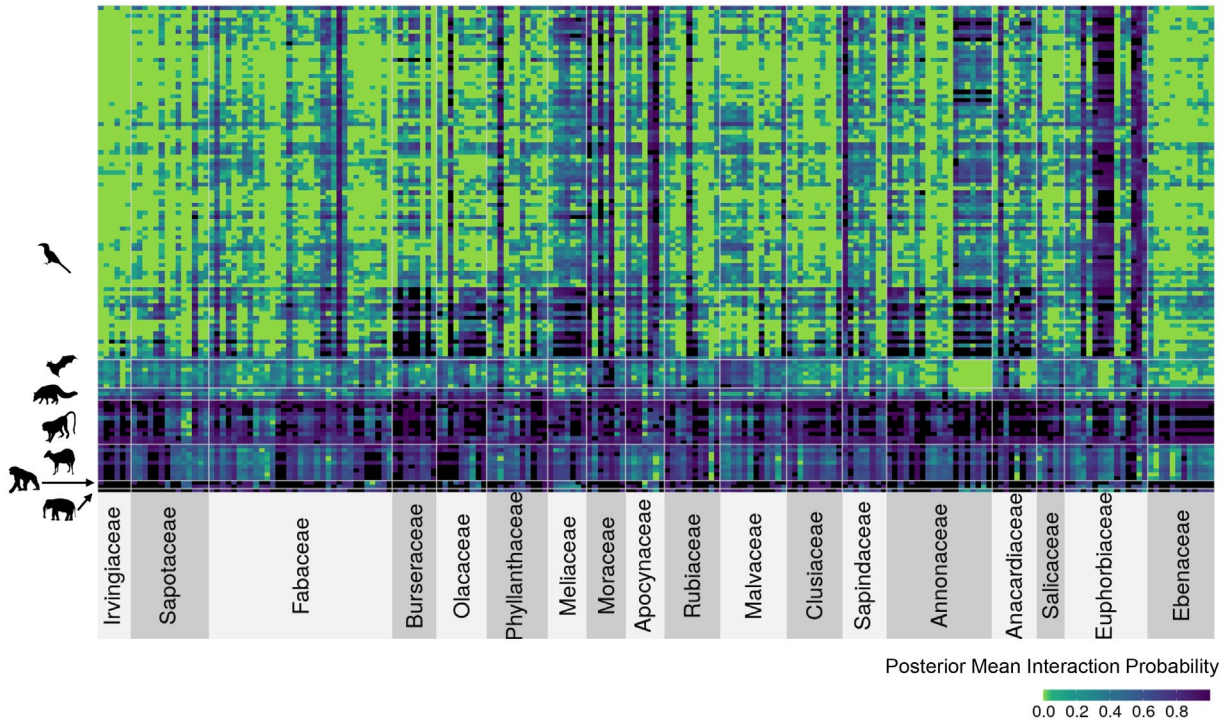


FIGURE 2 | Heatmap showing posterior mean probability of seed dispersal interactions in the imputed network; black rectangles indicate observed interactions. Animal taxa groups are organized by mean body mass, with lighter animals at the top and heavier animals at the bottom. Tree families are organized by mean AGB, with high-AGB families to the left and low-AGB families to the right. All animal and plant families with at least five representative species are displayed. Animal silhouettes are from PhyloPic.

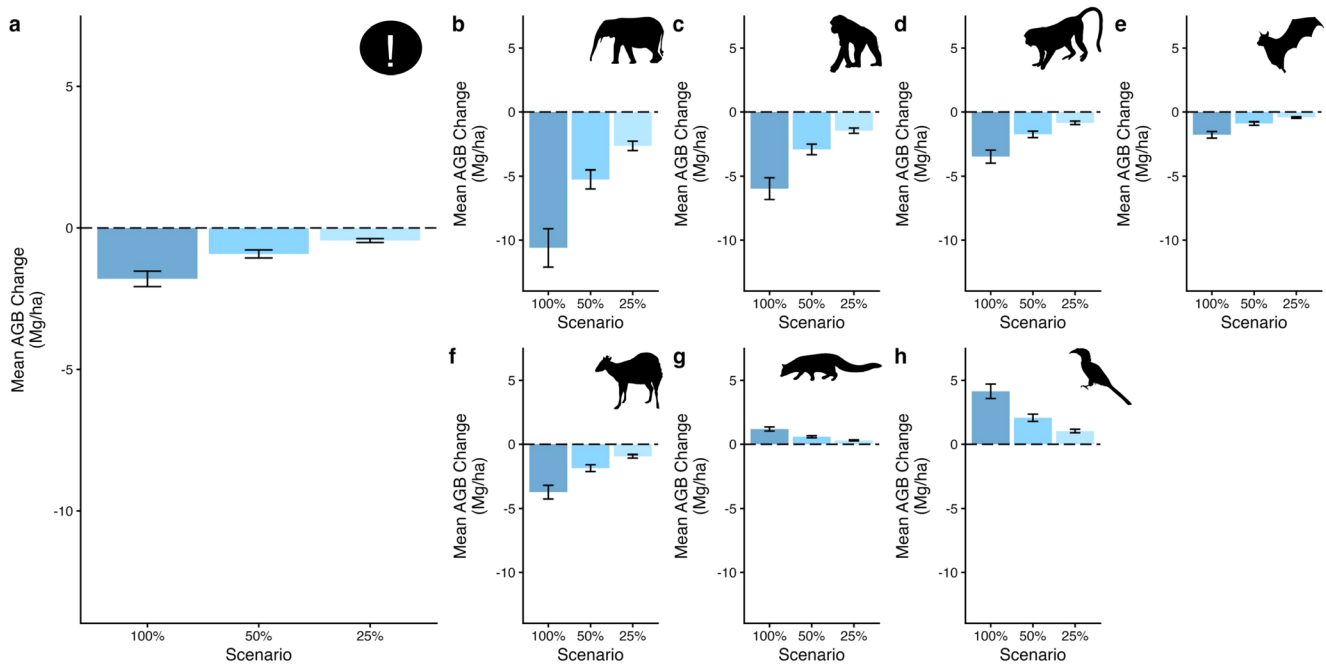


FIGURE 3 | Mean AGB change at the plot level given simulated faunal degradation of endangered species and for each taxon separately: (a) endangered species, (b) elephants, (c) apes, (d) monkeys, (e) bats, (f) ungulates, (g) carnivores, and (h) birds. The three panels represent results under three levels of degradation severity: 25%, 50%, and 100% loss of frugivores. The dashed vertical line represents no mean change in AGB; values to the right indicate mean AGB gain and values to the left indicate mean AGB loss. Error bars represent 95% confidence intervals. Animal silhouettes are from PhyloPic.

Birds and bats had low niche overlap with other taxa (Figure 4). Levin's niche breadths were variable among taxa (elephants: 16.3, apes: 23.3, monkeys: 28.2, bats: 6.2, ungulates: 21.0, carnivores: 21.2, birds: 5.4), but note that the number of species per taxonomic group varied considerably (Figure S1). Assuming complete compensation due to dietary redundancy, defaunation of endangered frugivores slightly increased AGB (Figure 5). For each taxon, the magnitude of AGB change was smaller when assuming complete compensation compared to not accounting for compensation.

3.4 | Geographic Patterns in AGB Change

Geographic patterns in AGB change from faunal degradation of endangered species were related to natural and anthropogenic environmental variation in Gabon. Simulated AGB changes from degradation of endangered species were positively associated with latitude (estimate = 1.346, $z = 5.6$, $p < 0.001$), elevation (estimate = 11.910, $z = 43.6$, $p < 0.001$), precipitation (estimate = 2.945, $z = 11.7$, $p < 0.001$), and forest exploitation status (secondary vs. primary forests; estimate = 8.159, $z = 15.5$,

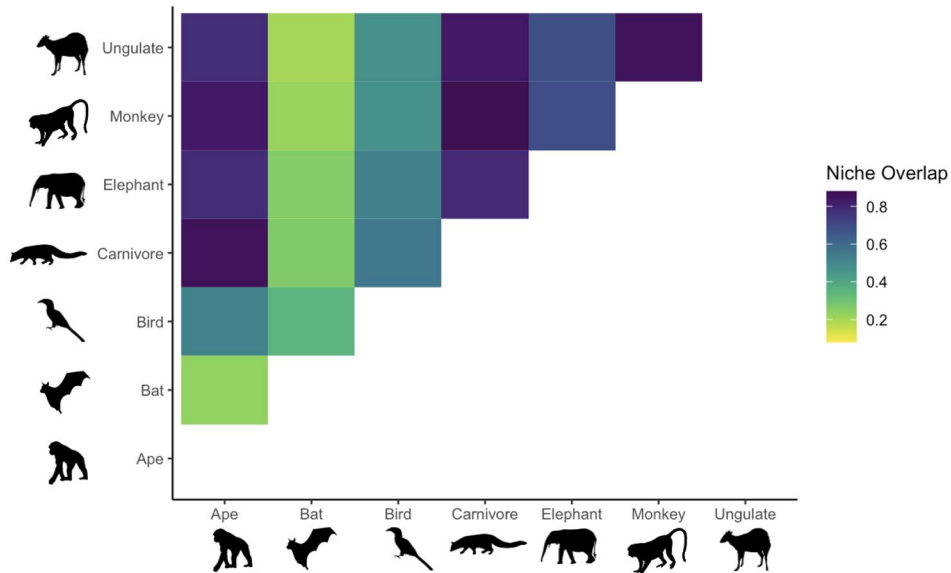


FIGURE 4 | Heatmap of Schoener's niche overlap between the seven frugivore taxa, where darker tiles correspond to higher niche overlap.

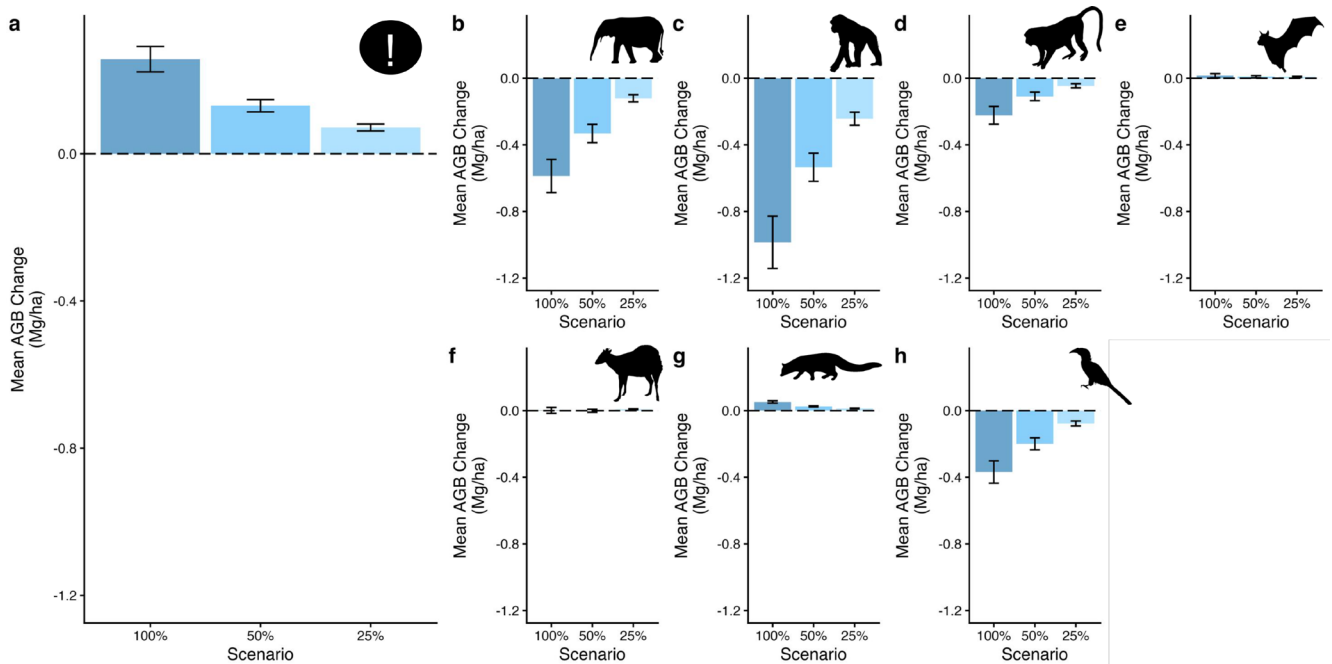


FIGURE 5 | Assuming complete compensation, mean AGB change at the plot level given simulated faunal degradation of endangered species and for each taxon separately: (a) endangered species, (b) elephants, (c) apes, (d) monkeys, (e) bats, (f) ungulates, (g) carnivores, and (h) birds. The three panels represent results under three levels of degradation severity: 25%, 50%, and 100% loss of frugivores. The dashed vertical line represents no mean change in AGB; values to the right indicate mean AGB gain and values to the left indicate mean AGB loss. Error bars represent 95% confidence intervals. Animal silhouettes are from PhyloPic.

$p < 0.001$) and negatively associated with distance to the nearest village (estimate = -3.548 , $z = 14.5$, $p < 0.001$; Figure 6). No significant differences were observed between primary and logged forests (estimate = 0.225 , $z = 0.4$, $p = 0.704$). The relationships between the characteristics of the plot and the simulated AGB change were largely consistent between the observed and imputed networks (Figure 6, see Table S6 for complete results). However, logged forests were negatively associated with AGB changes in the observed network (estimate = 3.073 , $z = 0.4$, $p < 0.001$). The results varied in taxon-specific faunal degradation scenarios (Figure S7, Tables S6, S7).

4 | Discussion

We applied a novel interaction imputation approach to quantify how faunal degradation influences AGB loss, addressing key uncertainties in seed dispersal. Our simulations estimate that defaunation (worst-case scenario, 100% faunal degradation) of endangered species would reduce AGB by 1.53 – 2.08 Mg/ha (Figure 3). These estimates likely represent a conservative lower bound because the model assumed that the 35.6% of tree individuals not identified to species level were not frugivore-dispersed. The decreased AGB due to simulated defaunation, especially of large-bodied taxa such as elephants and apes, supports our hypotheses. Furthermore, AGB change was dampened when accounting for dietary redundancy and was more severe in primary compared to secondary forests, also as expected. However, contrary to our expectations, AGB loss was due to tree size rather than wood density (Figure S3). Our simulated losses of AGB align with the findings from other tropical forests (Bello et al. 2015; Osuri et al. 2016; Chanthorn et al. 2019); by decreasing the establishment of seedlings (Rosin and Poulsen 2016), village-centered faunal degradation gradients (Beirne et al. 2019; Koerner et al. 2017) can perpetuate the loss of AGB. While defaunation can alter tree diversity and structure

(Harrison et al. 2013), its effects on AGB would occur over a long time scale (De Paula Mateus et al. 2018).

4.1 | Heterogeneity in Defaunation-Driven AGB Change

The effects of taxa-specific faunal degradation were variable and anthropogenic pressures may affect taxonomic groups differently (Koerner et al. 2017). The simulated extirpation of elephants and apes was particularly detrimental to AGB storage due to their role in dispersing diverse, carbon-rich trees (Figures 3, 4 and S3). We estimated that elephant defaunation alone would reduce AGB by 9.1 – 12.1 Mg/ha, a 3%–4% reduction in mean plot AGB (Figure 3). In addition, African forest elephants are also considered high-quality seed dispersers because they disperse seeds long distances—up to 101 km (Poulsen et al. 2021)—and defecate seeds in microsites favorable to recruitment (Campos-Arceiz and Blake 2011). Similarly, seed dispersal by apes can increase the probabilities of germination (Haurez et al. 2017) and aid in the recovery of logged forests (Haurez et al. 2016). Forest elephants and African apes are highly vulnerable to faunal degradation; forest elephants are Critically Endangered, while both ape species in our study (*G. gorilla* and *P. troglodytes*) are Endangered (IUCN 2024). Smaller-bodied frugivores such as duikers and bats may have a smaller impact on AGB maintenance compared to larger-bodied animals such as elephants because they tend to be less frugivorous and may disperse trees that are less carbon-dense than those dispersed by larger-bodied frugivores (Dubost 1984). But note that duikers can effectively disperse seeds in both logged and unlogged forests, promoting regeneration (Houngbégnon et al. 2023). Our taxa-specific faunal degradation scenarios emphasize different functional outcomes based on the extirpation of different frugivore species. However, animal extirpation based on broad taxonomic groups, particularly those with many species (Figure S1), is unlikely to occur in nature.

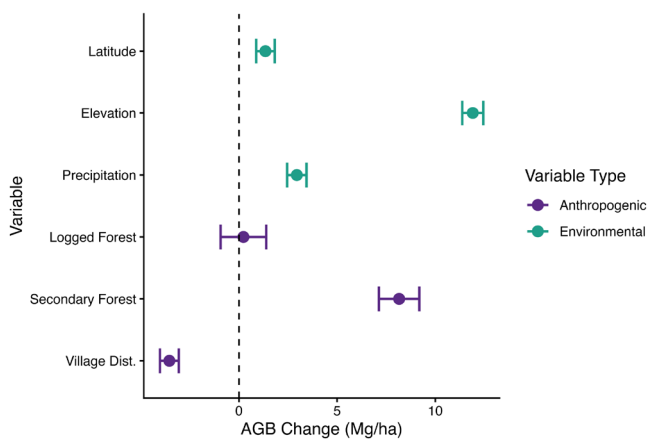


FIGURE 6 | Relationships between environmental variables and simulated AGB change (Mg/ha) for the 50% faunal degradation scenario, where endangered species were degraded. Bars are 95% confidence intervals based on the model averages. Secondary and logged forest values are compared to the basal factor primary forest. The dashed line represents no AGB change. Results were generated using the simulations that did not assume compensation due to dietary redundancy. Note that a positive effect indicates a positive change in AGB (i.e., less AGB loss).

Dietary overlap among frugivores may buffer AGB loss in the face of faunal degradation by compensating for lost dispersal services (Sekar and Sukumar 2013; García et al. 2014). Elephants and apes had a high niche overlap with other taxa, despite representing the fewest number of species per taxa (Figure S1), indicating the potential for seed dispersal compensation by other taxa. Therefore, a “rescue effect” may be possible, with overlapping diets mitigating AGB loss given faunal degradation of particular taxa. In the compensation scenarios, simulated AGB change was lower in magnitude for all taxa (Figure 5), compared to the scenarios where we did not assume dietary compensation (Figure 3). Notably, *complete* compensation led to increased AGB with faunal degradation of endangered species and decreased AGB with faunal degradation of birds. These results highlight the complexity of compensatory effects and the importance of the particular species with overlapping diets.

Complete functional compensation is unlikely because frugivores differ in their seed dispersal effectiveness (Schupp et al. 2017). For example, both elephants and apes are effective seed dispersers, moving viable seeds into favorable microsites, and elephants can move seeds over long distances (Campos-Arceiz and Blake 2011; Haurez et al. 2018). Frugivorous bats,

with their lower niche overlap with other taxa (Figure 4), are less likely to contribute to compensatory effects. It is improbable that either of the two extreme cases we present occur in nature; more likely, dietary redundancy may cause partial compensation, resulting in an intermediate AGB loss. The effectiveness of compensation depends on the DBH and WD of shared food plants, and more empirical studies are needed to quantify these effects. Furthermore, while our study considered seed dispersal mutualism as a driver of AGB in Gabon, other processes, such as trampling and browsing by elephants, also play a role in forest biomass dynamics (Berzaghi et al. 2023, 2019).

The vulnerability to AGB loss was also linked to natural and anthropogenic environmental characteristics (Figure 6). Areas with lower AGB due to existing environmental stresses, such as lower precipitation, may be more susceptible to dispersal limitation. However, primary forests and areas farther from villages (with relatively lower defaunation pressure) were more vulnerable to loss of AGB (Figure 6). Faunal degradation gradients surrounding villages drive the composition of the animal community in Gabon (Koerner et al. 2017), so forests farther from the villages may have a higher prevalence of animal-dispersed and carbon-rich plants. However, the relationship between environmental characteristics and AGB loss depended on the degraded taxa (Figure S7). For example, elephants, which are highly mobile and frequently consume cultivated plants, may be less affected by faunal degradation gradients compared to other taxa, such as monkeys (Koerner et al. 2017). Although relative abundances of mammals tend to be higher farther from villages, this is not always the case (Koerner et al. 2017), and logged forests may still serve as viable habitats for taxa such as apes and monkeys (Clark et al. 2009; Haurez et al. 2016). Our results also suggest that logged forests may not always be associated with a positive AGB change (Figure S3). Conservation efforts focused on sustaining frugivore populations in areas most vulnerable to AGB loss, such as low-elevation primary forests with low precipitation, could help sustain healthy ecosystem functioning.

4.2 | Limitations

Simulations are subject to model assumptions; our results represent likely trends in AGB maintenance rather than exact predictions. In particular, we did not account for seed dispersal effectiveness. Seed dispersal effectiveness depends on both the quality of dispersal (i.e., the likelihood of a dispersed seed resulting in a new plant recruit) and the quantity of dispersal (i.e., the number of seeds moved) (Schupp et al. 2017). In nature, heterogeneity in seed dispersal effectiveness can vary widely between ecological communities (Fricke et al. 2019). For example, in terms of seed dispersal quality, germination probability varies among and within species (DeSisto et al. 2025). Further, frugivores often exist on a mutualism-antagonism continuum, and some frugivory interactions may result in predation rather than seed dispersal. Defaunation can affect seed predation (Galetti et al. 2015), altering tree recruitment and AGB. In terms of seed dispersal quantity, quantitative data on Afrotropical seed dispersal are not available at the scale of our analysis. While extensive, the binary data used here may introduce bias into our results by disproportionately favoring rare interactions and overestimating dietary redundancy. Moreover, we were unable

to account for potentially disproportionate AGB change due to the loss of strong interactions, which cause an underestimation of the effects of defaunation. Future research on the effectiveness of community-wide seed dispersal will further refine our knowledge on the role of frugivores in maintaining ecosystem services such as carbon sequestration.

Our recruitment model assumed a random replacement of frugivore-dispersed trees with other trees in a given plot. Similar to previous studies (e.g., Bello et al. (2015), Razafindratsima et al. (2018), we specified a linear (1:1) relationship between faunal degradation and tree recruitment limitation. This simplifying assumption enables us to assess AGB change across diverse species and extensive spatial areas without the detailed demographic data necessary to detect complex recruitment patterns (such data are currently unavailable). However, a 1:1 replacement does not reflect important ecological processes, including size-structured dynamics, spatial dispersal patterns, and competition. Additionally, it is possible that new trees will not recruit, which would lead to an overestimation of AGB after defaunation. For example, through altered recruitment rates, climatic drivers such as drought can transform ecosystem types (Moss et al. 2024). Across Gabon, an average of 151 Mg/ha of AGB may be lost if there is failed recruitment of trees dispersed by endangered frugivores (sensitivity analysis in Figure S8). However, 100% recruitment failure is likely to be an implausible scenario. Research on alternative ecosystem states has suggested the possibility of a forest-savanna transition in Africa, but the evidence remains inconclusive (Higgins et al. 2024). Detailed long-term demographic data will be critical for further improving AGB change estimates and advancing a mechanistic understanding of the ecological consequences of defaunation.

Note that reduced tree recruitment induced by faunal degradation occurs over long time-scales; De Paula Mateus et al. (2018) estimated that the effects of defaunation on AGB in the Brazilian Atlantic forest would not occur until ~100 years after dispersal failure. Our results should not be interpreted as immediate consequences.

4.3 | Broader Ecological and Methodological Implications

Defaunation should be considered among other drivers of AGB change in tropical forests. Fire, human disturbance, and climate change all affect AGB storage in tropical forests. Fire emissions are the dominant driver of aboveground carbon loss in tropical forests worldwide (Feng et al. 2024). The history of human disturbance (e.g., logging and hunting) is the main driver of the change in AGB in the Brazilian Atlantic forest, followed by functional properties of forests and environmental conditions such as climatic water stress (Pyles et al. 2022). While defaunation may be a secondary driver of AGB change compared to direct habitat loss and disturbance, it confers unique long-term effects via seed dispersal and resulting tree community composition. Moreover, defaunation interacts with other drivers to affect carbon balances. Fire frequency, for example, has synergistic effects with faunal degradation on AGB in the Brazilian savanna (Maciel et al. 2021). Our results suggest that relationships between defaunation and other drivers such as forest disturbance

and climate are relevant for AGB storage in Gabon (Figure 6). Integrating defaunation into broader models of AGB change is necessary to understand the indirect, long-term mechanisms governing nutrient fluxes.

Imputing unobserved interactions can overcome pervasive sampling biases and improve our understanding of ecosystem functioning (Terry and Lewis 2020; Quintero et al. 2022; DeSisto et al. 2026). Seed-dispersing taxa like ungulates were underrepresented in the literature, which biased observed network simulations. Incomplete interaction data can produce inconsistent results; for example, mean AGB of ungulate-dispersed trees was slightly higher than that of nondispersed trees for the imputed network, while the opposite was true for the observed network alone (Figure S4). Although accounting for unobserved interactions likely improved the accuracy of our AGB change estimates, the imputed interactions likely remained incomplete. Despite inherent limitations in imputation, our robust approach is critical to advancing understanding of how faunal degradation affects ecosystem services, including but not limited to AGB. Our findings highlight the need to consider sampling bias in assessing species interactions and environmental change. Intact functioning of species interactions—not simply charismatic, easy-to-observe interactions—is important for the well-being of wildlife, plants, and people reliant on forest ecosystems.

4.4 | Conservation Insights and Conclusions

Accounting for ecological interactions across broad taxonomic groups is critical for conserving ecosystem functioning in tropical forests. In Gabon, the effects of faunal degradation on biomass varied by taxonomic group, with simulated elephant and ape degradation causing the greatest losses. To safeguard ecological functioning such as forest carbon storage, conservation efforts should protect the Critically Endangered *L. cyclotis* and *G. gorilla* as well as the Endangered *P. troglodytes* IUCN (2024). Although simulated defaunation of functionally unique taxa such as bats resulted in relatively minor AGB change (Figures 3 and 5), they provide other critical ecological services that merit conservation consideration, including insect control and pollination (Ramírez-Francel et al. 2022).

Spatial heterogeneity in the effects of defaunation on AGB should be considered in environmental management. Policies that preserve the integrity of species interactions in locations most vulnerable to loss of ecological functioning will help maintain AGB. For example, in our simulations, intact forests were more susceptible to AGB loss than secondary forests (Figure 6). Protecting frugivores in intact forests is therefore a priority for AGB maintenance. Nevertheless, sustaining the global carbon sink also requires the conservation of recovering secondary forests, which represent growing sources of forest carbon and dispersal potential (Heinrich et al. 2023). In addition to anthropogenic factors, climate variables such as precipitation predict frugivore interactions (DeSisto et al. 2026) and, consequently, AGB change (Figure 6). Frugivore seed dispersal, climate, and forest biomass are tightly coupled, underscoring the need to integrate faunal conservation into effective climate policy.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code supporting the results are archived at <https://github.com/jennifernoelle/COILplus> (imputation) and <https://github.com/camilledesisto/AfricaFrugivores> (simulation and subsequent analyses). Gabon plot data are subject to third party restrictions and are available from Le Ministère des Eaux, de la Forest, de la Mer, de l'Environnement. Restrictions apply to the availability of these data, which were used under licence for this study. Data are available from the corresponding author with the permission of Le Ministère des Eaux, de la Forest, de la Mer, de l'Environnement. Interaction data not included in the [Supporting Information](#) are from Durand-Bessart et al. 2023.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Number of frugivore species included in each taxon in the analysis. **Figure S2:** Number of tree fruit species consumed across the Gabon plots by the different frugivore taxa across Gabon. Gray bars represent observed interactions, and blue bars represent interactions based on the imputed frugivory network (including interactions where the interaction probability 0.5). **Figure S3:** Mean and 95% confidence intervals of (a) AGB, (b) wood density, and (c) diameter at breast height (DBH) between trees in our plots that were and were not dispersed by endangered species. Data represent values across tree individuals across all plots. Gray values indicate the observed network, and blue values indicate the imputed network. **Figure S4:** Mean and 95% confidence intervals of AGB between dispersed and non-dispersed trees in our plots for the different taxa groups. Grey values indicate the observed network, and blue values indicate the imputed network. **Figure S5:** Mean and 95% confidence intervals of DBH between dispersed and non-dispersed trees in our plots for the different taxa groups. Grey values indicate the observed network, and blue values indicate the imputed network. **Figure S6:** Mean and 95% confidence intervals of wood density between dispersed and non-dispersed trees in our plots for the different taxa groups. Grey values indicate the observed network, and blue values indicate the imputed network. **Figure S7:** Relationships between environmental variables and simulated AGB loss (Mg/ha) for the 50% faunal degradation scenarios for (a) elephants, (b) apes, (c) monkeys, (d) bats, (e) ungulates, (f) carnivores, and (g) birds. Bars are 95% confidence intervals based on the model averages. Secondary and primary forest values are compared to the basal factor primary forest. Blue values represent the imputed network, and gray bars represent the observed network; transparent values assume no compensation, and opaque values assume compensation. Dashed lines represent 0 AGB loss. **Figure S8:** Mean AGB change at the plot level given simulated faunal degradation of endangered species and assuming failed recruitment (i.e., no replacement after removal of frugivore-dispersed trees). Error bars represent 95% confidence intervals. **Table S1:** Summary table of AGB change (Mg/ha; mean, lower 95% confidence interval, and upper 95% confidence interval) for the observed network simulations. Values are rounded to the nearest integer. Results are included for the three faunal degradation scenarios (25%, 50%, and 100%). **Table S2:** Summary table of AGB change (Mg/ha; mean, lower 95% confidence interval, and upper 95% confidence interval) for the imputed network simulations. Values are rounded to the nearest integer. Results are included for the three faunal degradation scenarios (25%, 50%, and 100%). **Table S3:** Mean and 95% confidence intervals of AGB (Mg) between dispersed and nondispersed trees in our plots for the different taxa groups. **Table S4:** Mean and 95% confidence intervals of DBH (cm) between dispersed and nondispersed trees in our plots for the different taxa groups. **Table S5:** Mean and 95% confidence intervals of wood density (g/cm^3) between dispersed and nondispersed trees in our plots for the different taxa groups. **Table S6:** Summary of the relationship between mean AGB loss and environmental variables (estimate, z-value, and p-value) for the observed network. Results are based on 50% faunal degradation. **Table S7:** Summary of the relationship between mean AGB loss (Mg/ha) and environmental variables (estimate, z-value, and p-value) for the imputed network. Results are based on 50% faunal degradation. **Data S2. Data S3.**