Trade-Offs and Synergies Between Food and Fodder Production and Other Ecosystem Services in an Actively Restored Forest, Natural Forest and an Agroforestry System in Ghana

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Active restoration of degraded areas with multi-purpose tree species has been proposed as a measure to counter the losses from deforestation and mitigate consequences for local human communities. In a restoration project at a former mining site in Ghana, ecosystem services (ES) proxies in an actively restored forest were compared to a local agroforestry system and a natural forest. The results provide information about trade-offs and synergies between proxies of multiple ES(s). ES proxies were assessed according to the following categories: (a) food-tree ES: biomass of food and fodder trees, (b) other trees ES: biomass of fuelwood, medicine or mulch trees, (c) ES-providing arthropods: the number of detritivorous and predaceous arthropods, (d) carbon storage, and (e) tree diversity. Eight replicated plots with sizes of 20 m $\times$ 20 m were established in each forest type, and the following ES proxies were quantified: tree diversity was estimated as taxonomic richness of all trees with a diameter at breast height $\geq$ 10 cm in each plot. Tree species were then classified into ES categories (food, fodder, fuelwood, medicine, or mulch). Ground-dwelling arthropods were sampled for 10 weeks with five pitfall traps in each plot and categorized as decomposers and predators. Tree above-ground biomass was estimated based on the measured tree diameter, height, and specific wood density using an improved allometric equation. The above-ground biomass was later converted into carbon storage by assuming 50% of the above-ground biomass of each tree. ES proxies based on tree biomass were highest in the natural forest. Fodder, medicine, fuelwood, and mulch ES proxies were significantly higher in the restored forest than the agroforestry system. Decomposer arthropods were most dominant in the natural forest, followed by the restored forest and the agroforestry system. Predacious arthropods were more dominant in the restored forest than in the other forest types. Carbon storage was highest in the natural forest, followed by the agroforestry system and the restored forest. The actively restored forest took an intermediate position between the agroforestry system and the natural forest regarding values for all nine ES proxies. Out of the 14 possible relationships between food or

fodder and other ES proxies, five were significantly positive (synergies) with no observed trade-offs (significant negative relationships). High fodder production in the restored and natural forests went along with higher values of other biomass ES proxies and numbers of beneficial arthropods, while higher food biomass also correlated positively with numbers of decomposing arthropods. Our results document that active restoration of degraded sites provides a valuable framework to promote ES provision to local communities compared to agroforestry system, but at the cost of lower food and fuelwood biomass and carbon storage compared to natural forests.

INTRODUCTION

Deforestation and forest degradation in the tropics persistently continues due to unsustainable agriculture practices, mining, logging, construction of infrastructure, and urban expansion (Seymour and Harris, 2019). In 2019, about 11.9 million hectares of tree cover was lost in the tropics (Weisse and Goldman, 2020). Between 2010 and 2015, Ghana lost about 0.6% of its protected forest reserves because of factors such as illegal logging, encroachment for farming, and wildfire (Acheampong et al., 2019). Globally, deforestation is known as a major driver for the substantial loss of biodiversity and a decline in the provision of ecosystem services (ES) (Ciccarese et al., 2012) that affects numerous people worldwide [United Nations Convention to Combat Desertification [UNCCD], 2014]. The productivity of food systems that local communities depend on for their livelihoods is severely affected by ongoing deforestation (Nunoo et al., 2015).

One approach to revert losses from deforestation and mitigate consequences for local communities is active restoration, for example, with multi-purpose tree species that are capable of providing several ES (Reubens et al., 2011; Gamfeldt et al., 2013; Zemp et al., 2019). Deforestation often affects climatic variability leading to either prolonged drought or flooding which both impact food production (Chirwa and Adeyemi, 2019). Active restoration involves the direct planting of seeds or seedlings to aid the recovery of deforested and degraded lands to reach a pre-defined restoration aim (Morrison and Lindell, 2011; Crouzeilles et al., 2017). The success of restoration activities often is measured by improvement of soil fertility, carbon sequestration and the recovery of biodiversity in general (Chazdon, 2008). The benefits provided by restored ecosystems to local communities should be an additional focus of restoration programs (Erbaugh et al., 2020). Active forest restoration may contribute to the provision of ES (Bullock et al., 2011; Benayas and Bullock, 2012; Shimamoto et al., 2018; Damptey et al., 2020), defined as functions and products that benefit society (Millennium Ecosystem Assessment [MEA], 2005). The introduction of a new tree species or the loss of a certain species from a particular area may alter levels of various ES (Brockerhoff et al., 2017). Active restoration directly affects the establishment of tree species but further indirectly alters the composition of biotic communities in restored areas by its effects on functionally important organisms such as predators (e.g., spiders) of forest pests (e.g., silk and carpenter moths) or

decomposers (e.g., woodlice) which contribute to nutrient cycles (Fragoso and Varanda, 2011; Nicholls and Altieri, 2013; Kremen et al., 2018; Donkersley, 2019; Luong et al., 2019).

Ecosystem services include provisioning (e.g., food, fodder, energy), regulating (e.g., climate and pest regulation, carbon sequestration), and other indirect supporting services that are required for the production of the provisioning and regulating services (e.g., soil formation, nutrient cycling, primary production) [Millennium Ecosystem Assessment [MEA], 2005]. These services are associated to several groups of so called service-providing organisms performing related ecosystem functions (Luck et al., 2003). For instance, predators regulate crop pests as natural enemies, and detritivorous insects decompose dead organic matter contributing to nutrient cycling and thereby to improved agriculture production and carbon sequestration (Birkhofer et al., 2015). In addition to these services, ecosystems also produce some disservices (hereafter Ecosystem Disservice- EDS; Lyytimäki and Sipilä, 2009), as for example pest infestations may lead to trade-offs with ES. Insects, as very abundant invertebrates in tropical forests, produce a range of services and disservices with the potential for trade-offs and synergies (Dangles and Casas, 2019).

Today, restoration and conservation activities often focus on simultaneously enhancing more than one ES and avoiding trade-offs, thereby creating synergies to meet the diverse needs of society (Birkhofer et al., 2018, 2019; Shimamoto et al., 2018; Zeng et al., 2019). Ecosystem multifunctionality (EM) describes the ability of an ecosystem to supply multiple ecosystem functions simultaneously to satisfy different societal needs and preferences (Mander et al., 2007; Hölting et al., 2019). Manning et al. (2018) emphasized the importance of high biodiversity for the provision of ES because different species contribute to different ecosystem functions. The EM approach hence integrates measures of the relative supply of multiple ecosystem functions and services to evaluate multiple restoration targets based on a high number of individual indicators (Strobl et al., 2019). The multifunctional nature of ecosystems and the proposed multifunctionality approach cause the need to consider synergies and trade-offs between ES and functions (Raudsepp-Hearne et al., 2010; Gamfeldt et al., 2013; Peña et al., 2018). Berry et al. (2020), for example, discussed synergistic relationships between carbon storage and biodiversity, whereby the provision on one allowed for greater levels of the other. Damptey et al. (2020) also highlighted that higher tree biodiversity in actively restored

forests goes along with improved soil conditions, providing support for the assumption that higher biodiversity enhances EM. However, trade-offs, on the other hand, occur when the increase in one ES leads to a decrease in another ES (Bennett et al., 2009; Birkhofer et al., 2015; Lafond et al., 2017). Trade-offs has previously been observed between esthetic or cultural values of forests and timber production (Peña et al., 2018; Turkelboom et al., 2018) or between food provision and net primary productivity (Li et al., 2020).

In this study, we analyzed the levels and relationships between proxies of multiple ES in three different forest types (actively restored forest, agroforestry system, and natural forest in Ghana). The restored forest is a previous gravel mine site that was replanted with both native and exotic trees species after soil amendments (Damptey et al., 2020). ES proxies were assessed in the following categories: (a) food-related tree ES (biomass of food and fodder trees), (b) other trees ES (biomass of fuelwood, medicine or mulch trees), (c) ES providing arthropods (number of decomposers and predators), (d) carbon storage, and (e) tree diversity. The resulting data was then used to analyze the performance of multiple ES proxies in the three alternative forest types and to identify trade-offs and synergies between food-related ES (a) and other ES proxies (b–e). Major objectives of this study are to assess how active forest restoration 20 years after the initiation of restoration practices (i) determined levels of individual ES proxies compared to alternative forest types and if (ii) synergies or trade-offs between food-related and other ES proxies are evident across forest types. We hypothesize that active forest restoration enhances levels of food and fodder ES compared to the natural forest and to a lesser extent compared to the agroforestry system. However, high provision of food and fodder-related ES proxies is hypothesized to come at the cost of other ES proxies, like carbon storage or tree diversity.

MATERIALS AND METHODS

Study Area
The three forest areas are Terchire restoration area (actively "restored forest"), Bosomkese forest reserve ("agroforestry system") and Asukese forest reserve ("natural forest"). All forests are located in the Semi-Deciduous Forest Zone (SDFZ) of Ghana with a mean annual precipitation ranging between 900 and 1,500 mm and mean daily temperature of 25°C (**Figure 1**). The restored forest area was gravel mined on the surface for road construction until 1998 and in 1999 the area was subjected to active restoration by planting both indigenous and fast-growing exotic nitrogen-fixing tree seedlings at a planting distance of 2 m × 2 m and a density of 1,111 seedlings per hectare. The restored forest covers 15.4 ha (longitude 7°14.075′ W, and latitude 2°10.842′ N). The agroforestry system used to be a degraded forest reserve which was subjected to enrichment planting of trees inter-planted with both annual and perennial food crops (e.g., plantains, maize, cassava) to supply food and energy to local communities (longitude 2°14.782′ W, and latitude 7°6.338′ N). The natural forest is a protected forest reserve with strong restrictions (limited access to people and resource

use) against anthropogenic activity (longitude 2°31.107′ W, and latitude 7°8.469′ N) (Damptey et al., 2020).

Sampling Design
Eight plots (20 m × 20 m) were demarcated (systematically) and sampled in each of the three forest types. We counted, recorded, and identified all trees with a diameter ≥ 10 cm at breast height (dbh) to species level with the assistance of a local botanist and an experienced forest guard (member of the Ghana Forest Services Division) and a field manual (Hawthorne and Gyakari, 2006). The ecological significance of tree species was calculated based on the Importance Value Index (IVI = Relative density + Relative frequency + Relative abundance) measured as the sum of the relative density ($\frac{\text{No. of individuals of species A}}{\text{Total no. of individuals of all species}}$ × 100), frequency ($\frac{\text{Frequency of species A}}{\text{Sum of frequency values for all species}}$ × 100), and abundance ($\frac{\text{Total no. of individuals found}}{\text{No. of quadrats of occurrence}}$ × 100) of individuals per species (Curtis and McIntosh, 1950). Tree species were then classified into providers of tree-related ES (food, fodder, fuelwood, medicine or mulch trees) based on an existing database (Useful Tropical Plants Database[1]; Fern et al., 2014; **Table 1**). The biomass of each classified tree species was estimated based on the measured dbh (D), tree height (H), and specific wood density (p) based on an improved allometric equation for the tropical trees [In (AGB) = α + βIn (p × D^2 × H) + ε; (Chave et al., 2014)]. The specific wood density for each tree was obtained from several database or sources (**Supplementary Appendix 2**). Tree carbon stock was estimated by assuming 50% of the above-ground biomass of each tree (Lewis et al., 2013). The local richness of tree species at each plot was made comparable by rarefying species richness to the observed minimum of 11 trees with a diameter ≥ 10 cm at one study plot.

Ground-dwelling arthropods were continuously sampled for 10 weeks (June to August 2019), with five pitfall traps in each plot being emptied weekly. Pitfall traps were filled with 50:50 propylene glycol mixed with water and a few drops of odor-free detergent to reduce the surface tension (Schmidt et al., 2006; Pais and Varanda, 2010). Traps were then sheltered by small rain covers to minimize dilution by rain (Underwood and Quinn, 2010). Traps were left unused for 1 week prior to trapping to reduce any digging-in bias due to attraction of arthropods by cutting of roots (Greenslade, 1973). Pitfall trap samples were stored in 70% ethanol and later sorted into taxonomic groups according to available literature (order, suborder, or family), followed by classification into major feeding guilds (decomposers or predators).

Data Analysis
To statistically compare the resemblance between plots within and between forest types, we created a resemblance matrix showing all pairwise similarities between plots based on Gower similarities calculated from all nine ES proxies (**Table 1**; values of ES proxies were log (x+1) transformed prior to analyses). Gower similarities internally standardize all ES proxies individually to values ranging from 0 to 1 and this approach then allows for

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[1] http://tropical.theferns.info/
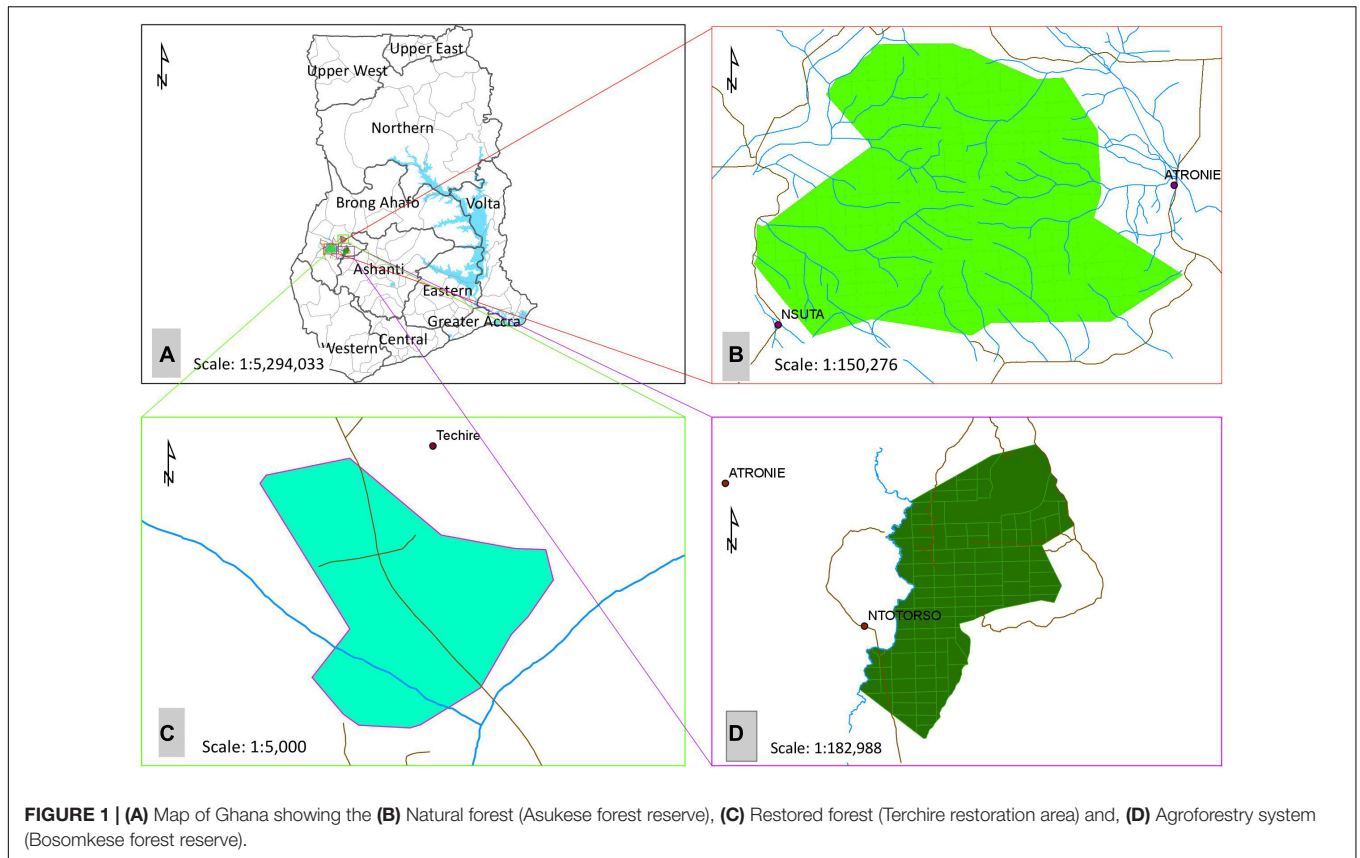
FIGURE 1 | (A) Map of Ghana showing the (B) Natural forest (Asukese forest reserve), (C) Restored forest (Terchire restoration area) and, (D) Agroforestry system (Bosomkese forest reserve).

TABLE 1 | Ecosystem Service (ES) proxies quantified in this study in major ES categories with rationale for their use in this study, examples and literature references supporting their classification.

ES category	ES proxy	Rationale	Examples	References
Provisioning	Food tree biomass	Production of fruits, nuts, leafy vegetables which serve as dietary and nutritional components	*Elaeis guineensis, Cola nitida, Dialium guineense, Terminalia catappa, Tetrapleura tetraptera, Artocarpus altilis, Mangifera indica*	Powell et al., 2015; Reed et al., 2017
	Fodder tree biomass	Leguminous tree parts as essential components of fodder resources for livestock	*Moringa oleifera, Leucaena leucocephala, Albizia ferruginea, Tetrapleura tetraptera*	Jasaw et al., 2017; Vandermeulen et al., 2018
	Medicine tree biomass	Used as traditional medicine and also raw materials for the pharmaceutical industry	*Tetrapleura tetraptera, Antidesma laciniatum, Moringa oleifera, Nesogordonia papaverifera*	Voeks and Rahmatian, 2004; Caballero-Serrano et al., 2019
	Fuelwood tree biomass	Supply of energy required for food production	*Cassia siamea, Celtis zenkeri, Leucaena leucocephala, Holarrhena floribunda*	Brockerhoff et al., 2017
	Mulch-tree biomass	Leguminous tree species used to improve soil fertility	*Albizia zygia, Leucaena leucocephala*	Kearney et al., 2019; Wagner et al., 2019
Regulating	Predator numbers	Predaceous arthropods that contribute to pest control	Spiders (Order: Araneae), Ground beetles (Order: Coleoptera, Family: Carabidae)	Brockerhoff et al., 2017
	Carbon storage	Storage of carbon dioxide in tree tissues	All tree species	González-Díaz et al., 2019; Hand et al., 2019
Supporting	Decomposer numbers	Detritivorous arthropods that contribute to organic matter decomposition	Millipedes (Orders: Glomerida and Julida)	Brockerhoff et al., 2017
Cultural	Tree richness (rarefied)	Spiritual and symbolic interaction with nature	All tree species	Brockerhoff et al., 2017; Kearney et al., 2019

the construction of resemblance matrices based on variables that are measured on different scales (e.g., biomass of medicine tree and abundance of predators). The resulting resemblance matrix was then analyzed with permutational analysis of variance (PERMANOVA) as the appropriate statistical method for distance-based analyses (Anderson et al., 2008). PERMANOVA is a common method to analyze resemblance matrices that can be based on uni- or multivariate data. PERMANOVA has the advantage over alternative parametric methods that it does not make assumptions about normality of the dependent data (as p-values are derived from permutations). We used PERMANOVA with identical model and design settings for all uni- and multivariate data to provide a standard analytical framework for all analyses. Multivariate data was further tested for homogeneity of dispersion using the PERMDISP routine as described in Anderson (2006). As a visual representation of the multivariate relationship between sample plots and also ES proxies, we show a non-metric multidimensional scaling ordination (NMDS) based on the GOWER resemblance matrix with vectors for all nine ES proxies superimposed based on Pearson correlation coefficients with site score in the NMDS.
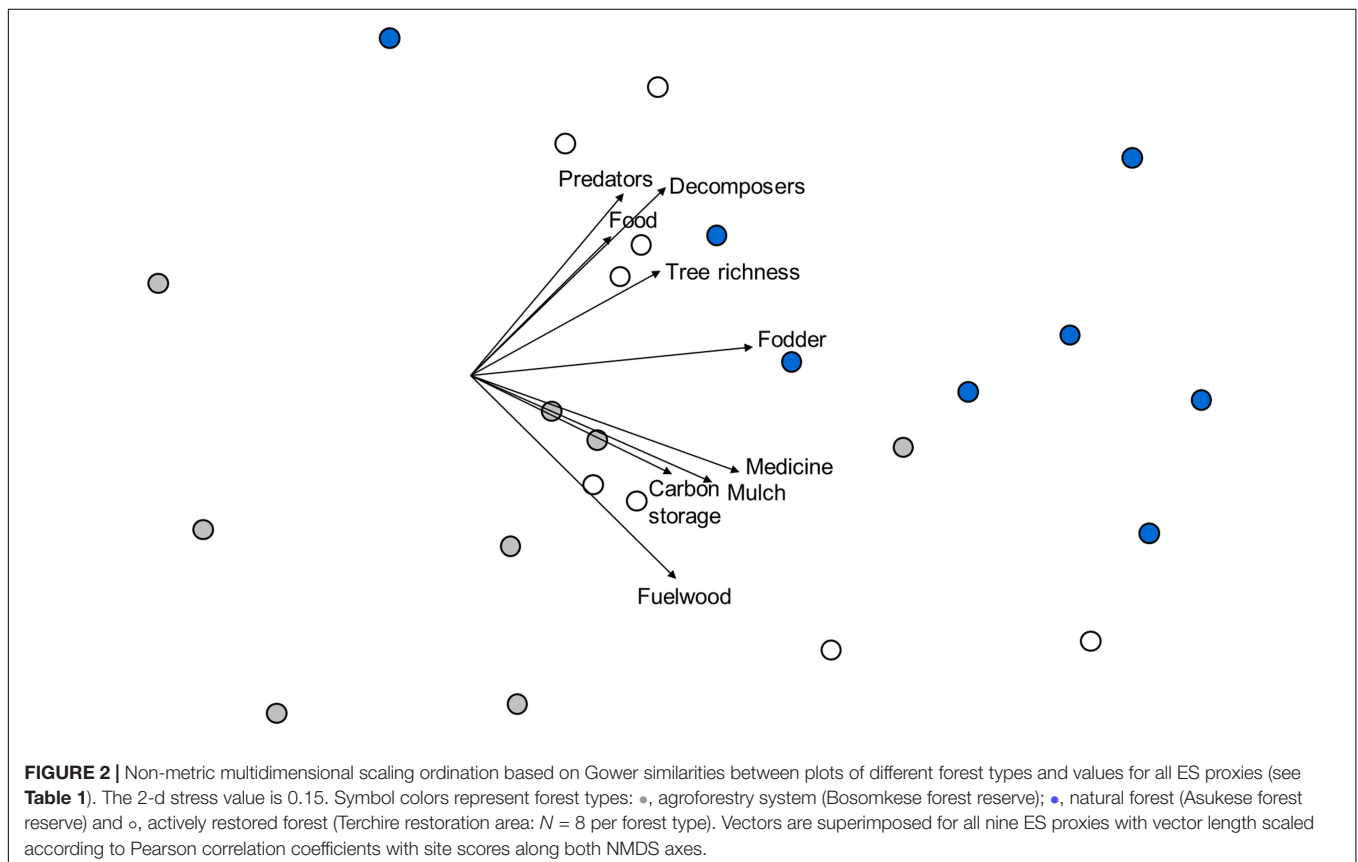
To then statistically compare levels of individual ES proxies related to tree biomass (food, fodder, medicine, mulch, and fuelwood tree biomass), ES providing arthropods (decomposer and predator numbers), carbon storage and tree diversity between actively restored forest and other forest type plots, we constructed resemblance matrices for each log (x+1)

transformed variable using Euclidean distances. All uni- and multivariate PERMANOVA analyses were performed with a one-factorial design (forest type: restored forest, agroforestry system, and natural forest) and 9,999 unrestricted permutation of the raw data (Anderson et al., 2008). In case of a significant PERMANOVA result, levels of the factor forest type were compared with pairwise PERMANOVA for post hoc testing. Correlations among food-related ES (food and fodder-tree biomass) and all other ES proxies were tested with Pearson correlations using the "ggubr" package (Kassambara, 2020). Test statistics for PERMANOVA models include F-values with degrees of freedom for the main factor and the residuals, pairwise post hoc PERMANOVA is given with t-values and correlation results are presented with Pearson correlation coefficients. Statistical analyses and visualizations were carried out with the Plymouth Routines in Multivariate Ecological Research (PRIMER vs. 7, with the PERMANOVA add-on; Clarke and Gorley, 2015) or Sigma Plot Version 12.0 (Systat Software, 2010).

RESULTS

Tree Structure

The restored forest had 43 species (**Supplementary Appendix 1**) with the most important species according to IVI being *Senna siamea* (IVI = 33.9), *Leucaena leucocephala* (IVI = 33.4), *Terminalia superba* (IVI = 24.3), and *Morinda lucida*

FIGURE 2 | Non-metric multidimensional scaling ordination based on Gower similarities between plots of different forest types and values for all ES proxies (see **Table 1**). The 2-d stress value is 0.15. Symbol colors represent forest types: ●, agroforestry system (Bosomkese forest reserve); ●, natural forest (Asukese forest reserve) and ○, actively restored forest (Terchire restoration area: N = 8 per forest type). Vectors are superimposed for all nine ES proxies with vector length scaled according to Pearson correlation coefficients with site scores along both NMDS axes.

(IVI = 13.4). The agroforestry system was characterized by major contributions of *Terminalia superba* (IVI = 52.8), *Ceiba pentandra* (IVI = 46.6), *Cedrela odorata* (IVI = 34.5), and *Triplochiton scleroxylon* (IVI = 22.1). The natural forest was also characterized by *Celtis mildbraedii* (IVI = 34.5), *Triplochiton scleroxylon* (IVI = 21.1), and *Nesogordonia papaverifera* (IVI = 17.5).

Forest Resemblance and Heterogeneity in ES Proxies

Based on a joint multivariate analysis of all ES proxies (**Table 1**), the three forest types differed significantly from each other (**Figure 2**; $F_{2,21}$ = 5.64; p = 0.001). Three clusters of points confirmed the differences in ES proxies, with the agroforestry system points separated from the restored forest or the natural forest. Dissimilarities were most pronounced between the natural forest and the agroforestry system (average pairwise Gower dissimilarity = 33.6%; t = 2.7; p = 0.014), followed by dissimilarities between the natural and the restored forest (30.8%; t = 2.2; p = 0.004) or the restored forest and the agroforestry system (30.1%; t = 2.1; p = 0.001) respectively. Predator and decomposer arthropods, food, and fuelwood biomass, showed a higher affinity to the restored forest. Tree richness and fodder biomass were more dominant in the natural forest, and a higher dominance of mulch biomass was recorded for the agroforestry system. The multivariate dispersion of ES proxy values was not significantly different between forest types ($F_{2,21}$ = 0.34; p = 0.736).

Food-Related ES Proxies

Forest types differed significantly in food tree biomass ($F_{2,21}$ = 4.13; p = 0.031). The food tree biomass in the natural forest was significantly higher than in the restored forest (t = 2.6; p = 0.022), with no significant differences between the agroforestry system compared to the natural or the restored forest (**Figure 3A**). Forest types differed significantly in fodder tree biomass ($F_{2,21}$ = 5.31; p = 0.013) with significantly lower biomass in the agroforestry system compared to the natural forest (t = 2.68; p = 0.020) and the restored forest (t = 2.67; p = 0.020) (**Figure 3B**). Characteristic food and fodder tree species in the restored forest were *Mangifera indica*, *Annona muricata*, *Terminalia catappa*, *Chrysophyllum perpulchrum*, and *Elaeis guineensis*. *Tetrapleura tetraptera*, *Chrysophyllum albidum*, and *Cola gigantean* were characteristic for the natural forest plots, while the agroforestry system plots were characterized by *Cola gigantean* and *Dialium guineense*.

Other ES Proxies

Forest types did not differ significantly in other tree related ES like fuelwood tree biomass ($F_{2,21}$ = 0.20; p = 0.820), medicinal tree biomass ($F_{2,21}$ = 1.81; p = 0.195), and mulch tree biomass ($F_{2,21}$ = 2.85; p = 0.079).
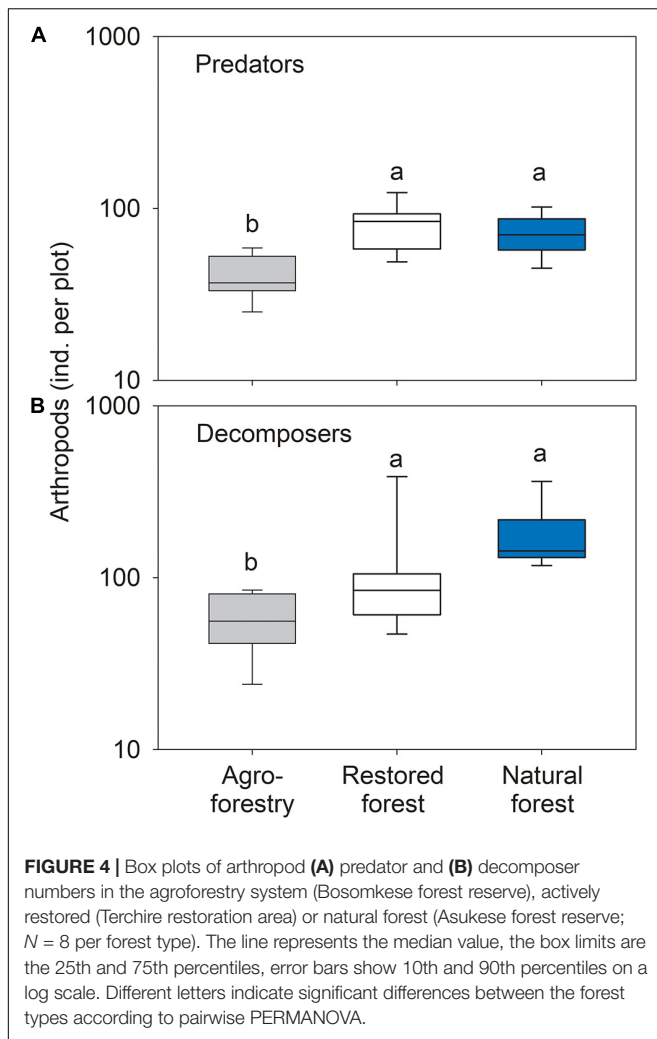
Forest types differed significantly in the number of predatory arthropods ($F_{2,21}$ = 12.66; P < 0.001). The agroforestry system plots had significantly fewer predators compared to the natural forest (t = 4.04; p = 0.003) and the restored

forest (t = 4.54; p = 0.001) (**Figure 4A**). The observed differences in the number of predatory arthropods were mainly driven by a higher number of individuals in the beetle families Staphylinidae and Histeridae, spider families Lycosidae, Corinnidae, Ctenidae, and in the order Opiliones in the restored forest compared to the agroforestry system. Individuals from the beetle families Carabidae and Dytiscidae, and the spider families Cyrtaucheniidae and Barychelidae were more abundant in agroforestry system compared to the restored forest.

The number of decomposer arthropods differed significantly between forest types ($F_{2,21}$ = 10.57; p = 0.001). Decomposer numbers were significantly higher in the natural forest (t = 5.64; p = 0.001) and the restored forest (t = 2.07; p = 0.042) compared to the agroforestry system plots (**Figure 4B**). The differences between restored forest and the agroforestry system were characterized by higher numbers of individuals in the beetle family Tenebrionidae and the millipede orders Glomerida, Julida, and Polydesmida in the restored forest plots. The natural forest plots had higher numbers of individuals in the millipede order Glomerida and the beetle family Tenebrionidae as well as more cockroaches (order Blattodea).
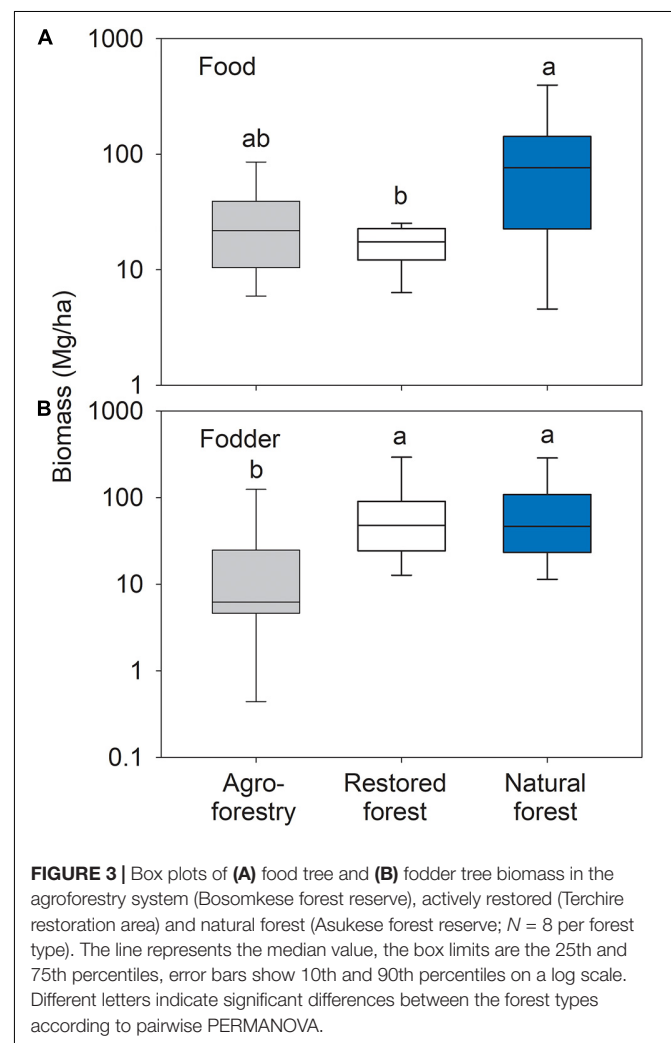
FIGURE 3 | Box plots of **(A)** food tree and **(B)** fodder tree biomass in the agroforestry system (Bosomkese forest reserve), actively restored (Terchire restoration area) and natural forest (Asukese forest reserve; N = 8 per forest type). The line represents the median value, the box limits are the 25th and 75th percentiles, error bars show 10th and 90th percentiles on a log scale. Different letters indicate significant differences between the forest types according to pairwise PERMANOVA.

FIGURE 4 | Box plots of arthropod (A) predator and (B) decomposer numbers in the agroforestry system (Bosomkese forest reserve), actively restored (Terchire restoration area) or natural forest (Asukese forest reserve; $N = 8$ per forest type). The line represents the median value, the box limits are the 25th and 75th percentiles, error bars show 10th and 90th percentiles on a log scale. Different letters indicate significant differences between the forest types according to pairwise PERMANOVA.

Carbon storage differed significantly between forest types ($F_{2,21} = 5.84$; $p = 0.011$) with significantly lower values in the restored forest compared to the agroforestry system ($t = 2.26$; $p = 0.004$) and the natural forest ($t = 3.12$; $p = 0.011$) (**Figure 5A**). Forest types differed significantly in rarefied tree species richness ($F_{2,21} = 6.53$; $p = 0.007$) with the restored forest ($t = 3.28$; $p = 0.001$) and the agroforestry system ($t = 3.22$; $p = 0.007$) having lower taxonomic richness than the natural forest plots (**Figure 5B**). The following tree species exclusively occurred in the natural forest plots: *Celtis aldolfi-frider, Celtis zenkeri, Chrysophyllum albidum, Corynanthe pachyceras, Dichapetalum madagascariense, Pterygota macrocarpa, Ricinodendron heudelotii,* and *Sterculia Oblongata.*

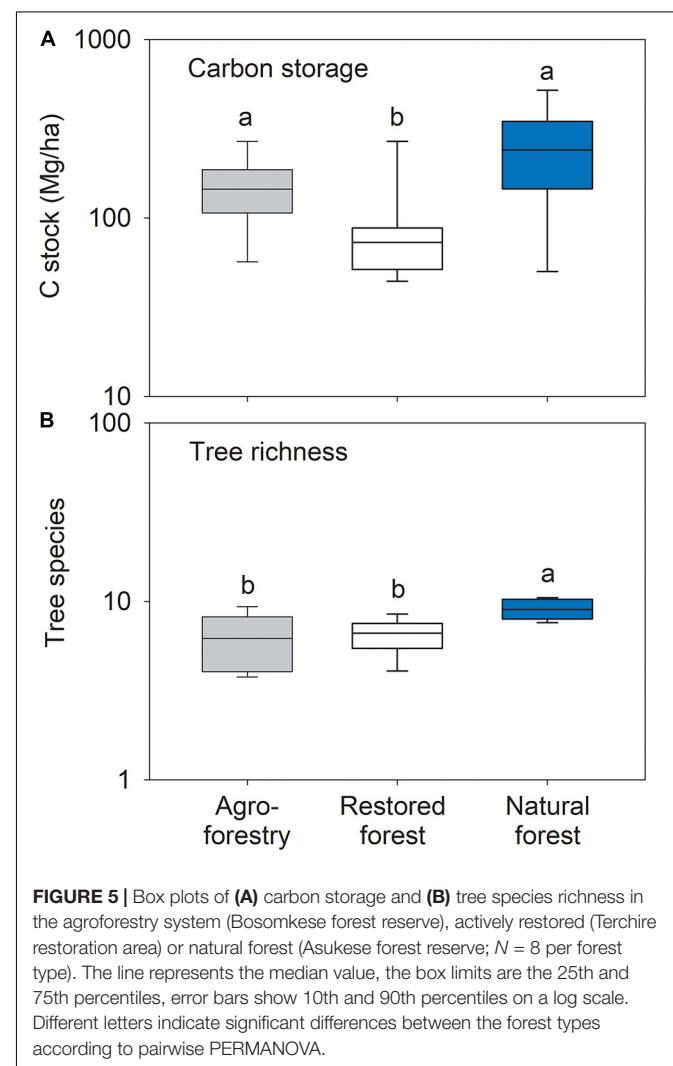## Trade-Offs and Synergies in ES Proxies

The natural forest had the highest relative values for all eight out of nine ES proxies, with carbon storage being the only exception and no apparent trade-offs between pairs of ES proxies (**Figure 6**).
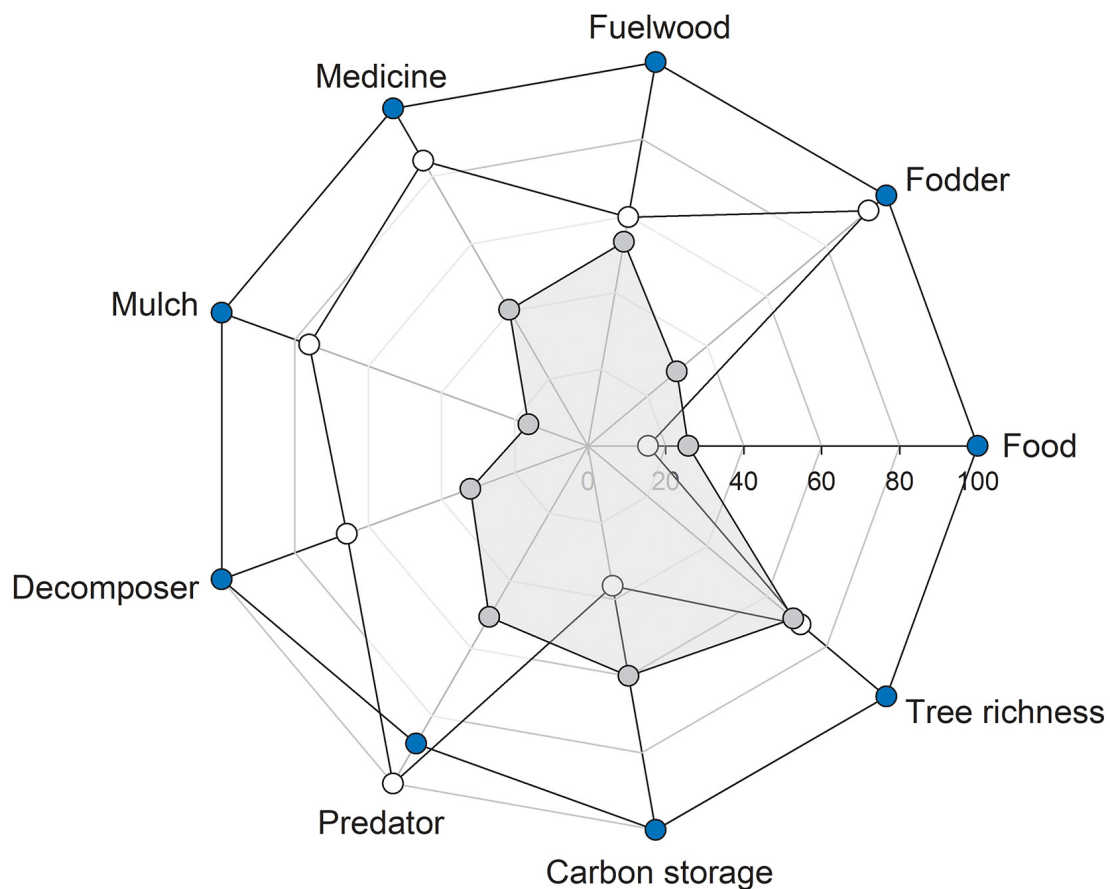
Out of 14 possible relationships between food or fodder tree biomass and the other seven ES proxies, five were significantly positive (synergies) with no significant negative relationships

(trade-offs). Food tree biomass was significantly correlated to the number of decomposer arthropods ($R = 0.43$, $p = 0.037$; **Figure 7A**). Fodder tree biomass was significantly correlated to medicine ($R = 0.78$, $p = 0.001$; **Figure 7B**) and mulch tree biomass ($R = 0.62$, $p = 0.001$; **Figure 7C**), and the number of decomposer ($R = 0.57$, $p = 0.003$; **Figure 7D**) and predatory ($R = 0.54$, $p = 0.006$) arthropods (**Figure 7E**).

DISCUSSION

Ecosystems with diverse tree communities are often superior in the provision of multiple ES compared to less diverse forests (Bullock et al., 2011; Gamfeldt et al., 2013; Brockerhoff et al., 2017). Trees contribute to provisioning (food, fodder, and fuelwood), regulating (pest regulation and carbon storage), supporting (habitat for organisms), and cultural (esthetic, symbolic, and religious) ES and determine the dynamics and functioning of forests (Blicharska and Mikusiński, 2014; Brockerhoff et al., 2017; Mori et al., 2017; Reed et al., 2017).

FIGURE 5 | Box plots of (A) carbon storage and (B) tree species richness in the agroforestry system (Bosomkese forest reserve), actively restored (Terchire restoration area) or natural forest (Asukese forest reserve; $N = 8$ per forest type). The line represents the median value, the box limits are the 25th and 75th percentiles, error bars show 10th and 90th percentiles on a log scale. Different letters indicate significant differences between the forest types according to pairwise PERMANOVA.

FIGURE 6 | Rader plot showing the relationship between ecosystem service proxies in forest types: •, agroforestry system (Bosomkese forest reserve); •, natural forest (Asukese forest reserve); and ○, actively restored forest (Terchire Restoration area: N = 8 per forest type). The highest average for each ES proxy across the three forest types was set to 100% and values for the same ES proxy in the other two forests were scaled accordingly.

Active restoration promoted selected ES (fodder tree biomass and predator numbers) compared to agroforestry in our study. However, levels of ES proxies in the natural forest were at least comparable or higher to the highest levels in agroforestry and actively restored forest plots for all ES proxies that differed significantly between forest types. Considering the ES proxies quantified in this study, optimal levels are only provided by the natural forest, followed by the actively restored forest which holds an intermediate position between natural and agroforestry plots showing the lowest benefits. Across forest types, several positive relationships between food and fodder tree biomass and other ES proxies became evident from multivariate analyses and highlight the potential to restore forests with the target to simultaneously promote multiple ES.

ES Proxies and Forest Types

Forest types offer different levels of ES due to specific properties of individual tree species (Gamfeldt et al., 2013; Fu et al., 2015; Bordt and Saner, 2019). Forest management (both agroforestry and active restoration) resulted in lower tree species richness compared to natural forest plots in our study, which may constrain the provision of biodiversity-based ecosystem functions due to negative effects on service-providing organisms (Hättenschwiler et al., 2005; Gessner et al., 2010; Conti and Díaz, 2013; Faucon et al., 2017; Albrich et al., 2018). Decomposer abundance indeed resembled the observed pattern for tree species richness between forest types, but estimated levels of carbon storage did not differ significantly between agroforestry and natural forest plots. Active restoration, on the other hand, resulted in relatively high fodder tree biomass and a large number of predatory organisms. The high number of predatory organisms in actively restored forest plots and natural forests may be a response of these beneficial arthropods to more diverse vegetation often coupled with higher prey availability (structure-mediated and resource-mediated effects, Diehl et al., 2012). Natural forest plots indeed had the highest tree species richness and potentially offered diverse habitat structure supporting predatory organisms (see also Bianchi et al., 2006; Staab and Schuldt, 2020). Actively restored forest plots on the other hand did not have significantly richer tree communities compared to agroforestry plots. A previous study, however, showed that actively restored forest plots had a more complex topsoil and soil surface structure than agroforestry plots (Damptey et al., 2020) thereby potentially also supporting higher predator numbers.
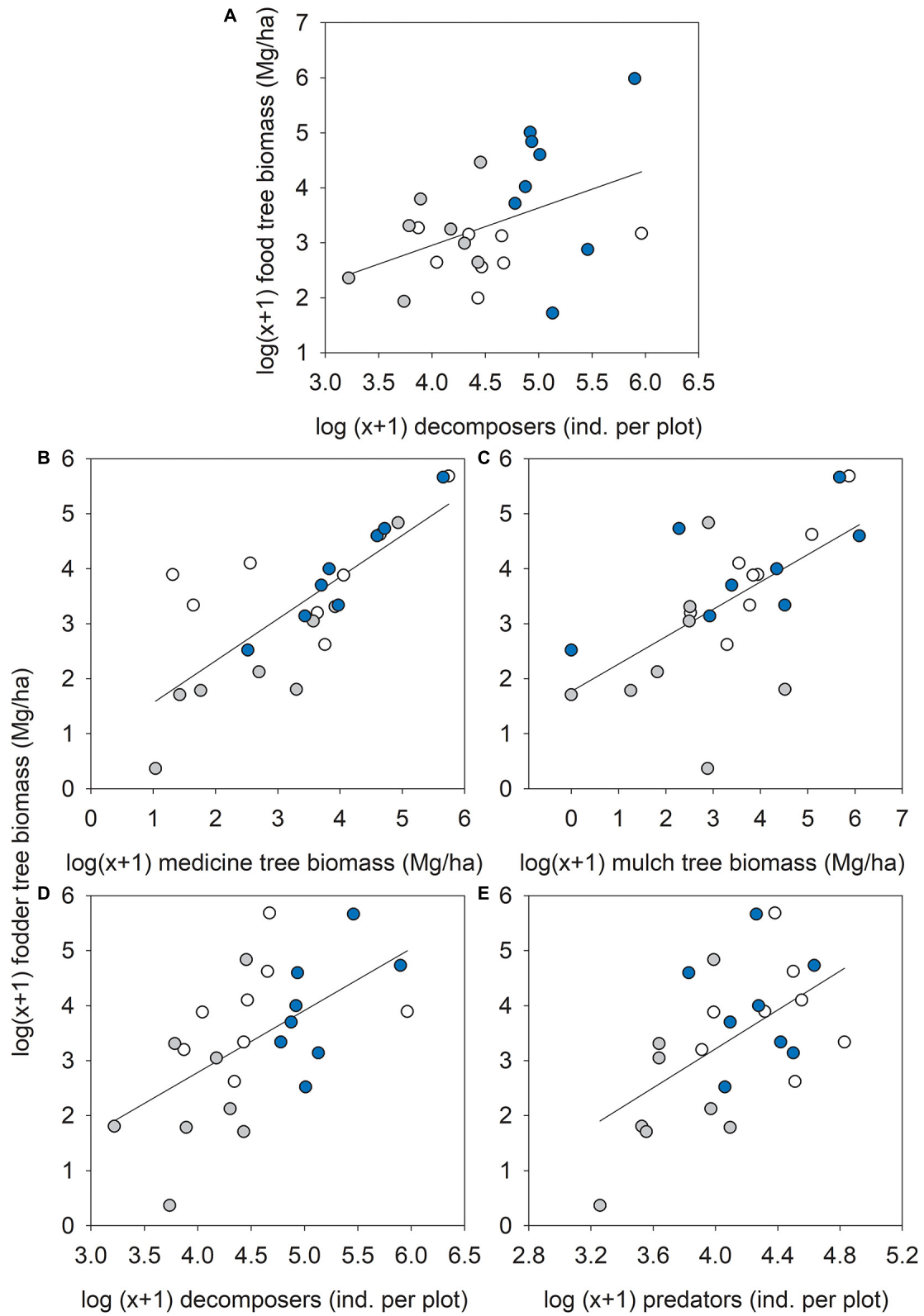
FIGURE 7 | Relationship between **(A)** food tree biomass and decomposer arthropod numbers, or fodder tree biomass and **(B)** medicine tree biomass, **(C)** mulch tree biomass, **(D)** decomposer, and **(E)** predatory arthropod numbers across forest types: •, agroforestry system (Bosomkese Forest Reserve); •, natural forest (Asukese Forest Reserve); and ○, actively restored forest (Terchire Restoration area; N = 8 per forest type).

Agroforestry programs in the tropics often aim for an increasing timber or food production (Waldron et al., 2017; Santoro et al., 2020). The observed significantly higher food tree biomass in agroforestry plots compared to actively restored forest plots is therefore not surprising. This benefit, however, comes at the cost of significantly lower numbers of beneficial arthropods. Previous studies highlighted the important role of soil invertebrates as key drivers of soil functioning and ES provision (Lavelle et al., 2006; Birkhofer et al., 2011; Soliveres et al., 2016) making them valuable indicators of overall soil quality (Fu et al., 2015). Hence, the low decomposer numbers in agroforestry plots should be perceived as a warning sign for the limited value of these agroforestry approaches in the study region (see also Damptey et al., 2020). However, in contrast to our hypothesis, agroforestry plots still produced a higher food tree biomass compared to actively restored forest plots. Restoration approaches need to be optimized toward higher levels of food tree growth if food supply is relevant for the region.

Relationships Between Food-Related and Other ES

Human societies demand different ES which are often competing with each other, and thus, trade-offs are more common than synergistic relationships in changing ecosystems (Fu et al., 2015). In our comparison of active restoration to other forest types, we observed several synergies between food or fodder tree biomass and other ES proxies, but no trade-offs which is in contrast to our hypothesis. Food tree biomass increased with the number of decomposer arthropods, whereas fodder tree biomass correlated with medicine and mulch tree biomass and decomposer or predatory arthropod numbers. High decomposer activity accelerates litter decomposition and remobilizes nutrients essential for the growth of plants (Kitz et al., 2015; Eisenhauer et al., 2018; Maldonado et al., 2019). Decomposers have been found to contribute to reduced soil compaction and increased soil aeration which is essential for crop production (Manning et al., 2016). These active contributions of decomposing arthropods to primary production explain their positive correlation to food and fodder tree biomass. Fodder tree biomass also correlated positively with predatory organism numbers, which may result from the presence of different ecological niches for predatory organism or the presence of preferred tree species in plots with higher fodder tree biomass. Diverse forests often also harbor greater predator (natural enemies) abundance which may simultaneously result in improved control of pests (Staab and Schuldt, 2020).

The fact that the majority of tree species recorded had multiple purposes to some extend partly explains the positive relationships between different tree-related ES proxies. For instance, *Moringa oleifera* serves well as food, fodder, and plant-derived medicine species, *Tetrapleura tetraptera* is also used as medicine, for food and fodder, *Leucaena leucocephala* serves as fodder for livestock, mulch for crop cultivation and fuelwood for household cooking while *Senna siamea* is known for its medicinal, fodder, and fuelwood uses in the study regions.

CONCLUSION

Our comparison of ES proxies between actively restored forest, agroforestry and natural forest plots highlighted the high value of natural forests for the provision of ES in the study region. However, creating a forest composition resembling the natural forest plots through post-mining restoration approaches may not be a realistic goal. Alternative restoration practices are therefore needed to optimize the provision of ES and active restoration seems to provide a viable option, as levels of fodder tree biomass, predator and decomposer numbers were relatively high. However, future active restoration approaches should be optimized toward higher levels of food tree biomass that are at least comparable to levels in agroforestry plots and would support local human communities. The monitoring of ES proxies in actively restored forests should further continue as the trajectory of these plots over time is unknown.

DATA AVAILABILITY STATEMENT

The datasets analysed for this study are available at: https://doi.org/10.6084/m9.figshare.14402120.

AUTHOR CONTRIBUTIONS

FD, ER, and KB designed the study. FD performed field and laboratory work. All authors contributed to the data analysis, interpretation, writing of the manuscript, and approved the submitted version.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.630959/full#supplementary-material

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