

**Effects of forest restoration on ecosystem attributes in a post-mining area
in Ghana**

A thesis approved by the Faculty of Environment and Natural Sciences at the
Brandenburg University of Technology Cottbus-Senftenberg in partial fulfilment of
the requirement for the award of the academic degree of Doctor of Philosophy
(Ph.D.) in Environmental Sciences

by

Master of Science

Frederick Gyasi Damphey

from

Akwatia, Eastern Region, Ghana

Supervisor: Prof. Dr. Klaus Birkhofer

Supervisor: Prof. Dr. Thomas Raab

Day of the oral examination: 20th February, 2023

DOI:<https://doi.org/10.26127/BTUOpen-6258>

Thesis committee

Chairperson: apl. Prof. Dr. Manfred Wanner

Fachgebiet Ökologie

Brandenburg University of Technology, Cottbus-Senftenberg

1st examiner: Prof. Dr. Klaus Birkhofer

Fachgebiet Ökologie

Brandenburg University of Technology, Cottbus-Senftenberg

2nd examiner: Prof. Dr. Thomas Raab

Lehrstuhl Geopedologie und Landschaftsentwicklung

Brandenburg University of Technology, Cottbus-Senftenberg

Member: PD Dr. rer. Nat. habil. Udo Bröring

Fachgebiet Ökologie

Brandenburg University of Technology, Cottbus-Senftenberg

Secretary: Dr. El Aziz Djoudi

Fachgebiet Ökologie

Brandenburg University of Technology, Cottbus-Senftenberg

Declaration

I hereby declare that this thesis has not been previously published or written by another person; neither has it been submitted nor accepted for any other academic award. It is the result of my original work carried out at Brandenburg University of Technology Cottbus-Senftenberg, Germany, within the framework of the Ph.D. Programme “Environmental and Resource Management”. All materials from other sources have been duly and adequately acknowledged.

Copyright notice

Chapters III, IV and VI have been published in peer-reviewed journals, namely *Land* (copyright with MDPI), *Forests* (copyright with MDPI), and *Frontiers in Forests and Global Change* (copyright with Frontiers Media), respectively. **Chapter V** has been resubmitted after revision for publication in *Community Ecology* (copyright with Springer). All published articles are available (open access) under the Creative Commons Attribution Licence. Thus use, distribution and reproduction of the work is permitted, provided that the original published work is properly cited.

Chapter III: Dampney, F. G., Birkhofer, K., Nsiah, P. K., & de la Riva, E. G. (2020). Soil properties and biomass attributes in a former gravel mine area after two decades of forest restoration. *Land*, 9(6), 209.

Chapter IV: Dampney, F. G., Birkhofer, K., Oliveras Menor, I., & de la Riva, E. G. (2022). The functional structure of tropical plant communities and soil properties enhance ecosystem functioning and multifunctionality in different ecosystems in Ghana. *Forests*, 13(2), 297.

Chapter V: Dampney, F. G., El Aziz Djoudi, & Birkhofer, K. (2022), Effects of post-mining forest restoration and alternative land-uses on ground-dwelling arthropods in Ghana. (Manuscript resubmitted after revision for publication in *Community Ecology*).

Chapter VI: Dampney, F. G., de la Riva, E. G., & Birkhofer, K. (2021). 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. *Frontiers in Forests and Global Change*, 4, 630959.

Table of Contents

Thesis committee	i
Declaration	ii
Copyright notice.....	iii
Summary	vi
Zusammenfassung	ix
List of abbreviations.....	xiii
Chapter I: General Introduction.....	1
Chapter II: General methodology.....	10
2.1 Study areas	10
2.2 Sampling design.....	13
2.3 Chapter synthesis.....	16
References.....	18
Chapter III: Soil properties and biomass attributes in a former gravel mine area after two decades of forest restoration.....	28
Chapter IV: The Functional Structure of Tropical Plant Communities and Soil Properties Enhance Ecosystem Functioning and Multifunctionality in Different Ecosystems in Ghana.....	62
Chapter VI: 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.....	144
Chapter VII: General Discussion.....	180
Main findings	180
Conclusion.....	187
References	190
Appendices.....	197
Acknowledgements	198
List of publications	201

List of figures

Figure 1: Land-use types studied for ecosystem attributes..... 6
Figure 2: Map of Africa showing Ghana with its regions 11
Figure 3: Flowchart showing the measured ecosystem attributes 14
Figure 4: Synthesis of the thesis..... 17

List of table

Table 1: Levels of biodiversity attributes and ecosystem services for land-use types..... 189

Summary

Approaches to restore post-mining areas should provide sustainable solutions for recovering biodiversity and ecosystem services in Afrotropical regions that experience massive deforestation. Key components that are impacted by surface mining activities and that restoration intervention should therefore target are biodiversity attributes (here, plants and arthropods) and ecosystem service provisioning. Previous studies focused on the effects of restoration activities on biodiversity and ecosystem services in other parts of the world, but the consequences of restoration decisions in post-mining areas in the Afrotropical region (here Ghana) remain understudied. To this end, I assessed levels of soil properties, biodiversity and ecosystem service in a post-mining area after two decades of active forest restoration by comparing them to attributes of the surrounding dominant land-use types and an unrestored former mine.

I hypothesized that (i) the interventions applied to restore and manage a post-mining area improve ecosystem attributes (for example, the soil status and tree diversity) beyond conditions observed in unrestored gravel mines or in alternative dominant land-use types (agriculture and agroforestry plantations) and even reaching levels comparable to natural reference forest (**Chapter III**), (ii) soil conditions and the functional structure of tree communities drive ecosystem functions and multifunctionality in land-use types with trees, with highest multifunctionality levels in the restored and natural forests (**Chapter IV**), (iii) the structure of tree communities coupled with pronounced climatic seasonality support a higher number of arthropods and arthropod functional groups particularly in the wet season and in structurally heterogeneous land-use types (restored and natural forests) (**Chapter V**), and (iv) active forest restoration enhances the levels of ecosystem service provision similar to the reference forest with possible trade-offs or synergies among individual ecosystem services across forest types (**Chapter VI**).

Chapter I provides an introduction to deforestation, the causes and effects on local livelihood and biodiversity with particular reference to Ghana's rainforest and further highlights global and national initiatives, including active forest

restoration, to reverse or minimize the impacts of tropical deforestation. In addition, **Chapter I** highlights the benefits of restoration for local human communities and biodiversity, and **Chapter II** then details the methodological approaches applied for sampling ecosystem attributes.

In **Chapter III**, I investigated soil properties in addition to below and above-ground biomass of trees in an active post-mining restoration area. I compared these ecosystem's attributes to levels in four alternative land-use types representing a gradient from an unrestored former mining site, to an agricultural field, to an agroforestry plantation and a natural forest as reference. The characteristic soil attributes for the restored forest (RF) were not significantly different from those in the natural reference forest (NF), except for bulk density (1.36 vs 1.17 gcm⁻³) and base saturation (92.26 vs 95.19%), but differed significantly from attributes in all other land-use types. The results indicate a successful restoration trajectory for soil attributes 20 years after restoration initiation. The improved soil conditions in the restored forest led to the development of dense vegetation cover, which fostered carbon sequestration through both above-and-below ground biomass increases.

In **Chapter IV**, I tested whether the functional structure of tree communities affects the provision of ecosystem services in different land-use types. For functional composition, both the leaf economic spectrum and the seed mass dimensions separated different land-use types. The natural forest was dominated by acquisitive plant species, and the non-natural forest showed a higher variation in functional space (140.19 sd³ for agroforestry plantation and 109.40 sd³ for restored forest compared to 21.45 sd³ in the natural forest). The functional richness of tree communities was best explained by the soil conditions and was positively related to the provision ecosystem service proxies and multifunctionality across all forest types.

In **Chapter V**, I addressed the research question on how post-mining restoration affects arthropod communities compared to a natural reference forest, alternative land-use types and an unrestored former mining site. Communities of ground-active arthropods differed significantly between land-use types depending

on the season. Arthropod communities of the restored forest plots had an intermediate position between the agroforestry plantation and the natural forest in terms of their taxonomic composition. The unrestored former mining site had a unique and significantly poorer community composition compared to the other land-use types. These variations in arthropod communities between land-use types were best explained by vegetation attributes, mainly taxonomic composition and diversity of tree communities and deadwood volume.

By quantifying the various ecosystem attributes in the field and transforming them into ecosystem service proxies, I could primarily identify synergies with no apparent trade-off between ecosystem services across the forest land-use types (**Chapter VI**). For example, food tree biomass simultaneously increased with the number of litter decomposing arthropods indicating a synergetic relationship between supporting ecosystem services and food provisioning. In addition, fodder tree biomass simultaneously increased with the number of predaceous arthropods.

This thesis contributes to a better understanding of the effects of active restoration at post-mining sites on relationships between soil and biodiversity attributes and their influence on ecosystem service provision in a severely understudied region that suffers from massive deforestation. The active restoration interventions established 20 years ago at a former mining site created a forest ecosystem that resembles the natural reference forest more than any of the alternative land-use types. However, it remains unclear how this system will change in the future and if a simultaneous provision of high soil quality and biodiversity and ecosystem service provision can successfully be accomplished in the long term.

Keywords: arthropods, biodiversity, ecosystem services, Ghana, post-mining restoration

Zusammenfassung

Renaturierungskonzepte von Bergbaufolgelandschaften bieten nachhaltige Lösungen für die Wiederherstellung der biologischen Vielfalt und der Ökosystemleistungen, insbesondere für von massiver Entwaldung betroffenen Regionen wie der Afrotropis. Die wichtigsten Komponenten, die durch den Tagebau beeinträchtigt werden und auf die Wiederherstellungsmaßnahmen daher abzielen sollten, sind Merkmale der biologischen Vielfalt (hier Pflanzen und Arthropoden) und die Bereitstellung von Ökosystemleistungen. Frühere Studien konzentrierten sich auf die Auswirkungen von Renaturierungsmaßnahmen auf die biologische Vielfalt und die Ökosystemleistungen in anderen Teilen der Welt und, die Folgen von Renaturierungsentscheidungen in Bergbaufolgelandschaften in der afrotropischen Region (hier Ghana) sind nicht ausreichend untersucht. Zu diesem Zweck wurde die Bodeneigenschaften, die biologische Vielfalt und die Ökosystemleistungen in einem Bergbaufolgegebiet nach zwei Jahrzehnten aktiver Waldsanierung bewertet, indem sie mit den Eigenschaften der umliegenden vorherrschenden Landnutzungstypen und einer nicht sanierten ehemaligen Mine verglichen.

Auf der Grundlage des oben genannten Ziels der Studie wurden folgende Hypothesen aufgestellt, dass (i) die Maßnahmen zur Wiederherstellung und Bewirtschaftung einer Bergbaufolgefläche die Ökosystemeigenschaften (z. B. den Bodenzustand und die Baumvielfalt) über die Bedingungen hinaus verbessern, die in nicht sanierten Kiesgruben oder in alternativen dominanten Landnutzungstypen (Landwirtschaft und agroforstliche Plantagen) beobachtet wurden, und sogar ein Niveau erreichen, das mit dem natürlicher Referenzwälder vergleichbar ist (siehe Kapitel III), (ii) die Bodenbedingungen und die funktionelle Struktur der Baumgemeinschaften die Ökosystemfunktionen und die Multifunktionalität in Landnutzungstypen mit Bäumen bestimmen (siehe Kapitel IV), (iii) die Struktur der Baumgemeinschaften in Verbindung mit einer ausgeprägten klimatischen Saisonalität eine höhere Anzahl von taxonomischen und funktionellen Arthropodengruppen fördert, insbesondere in der Regenzeit und in strukturell heterogenen

Landnutzungstypen (wiederhergestellte und natürliche Wälder) (Kapitel V), und (iv) die aktive Wiederherstellung von Wäldern das Niveau der Bereitstellung von Ökosystemdienstleistungen ähnlich dem des Referenzwaldes verbessert, mit möglichen Kompromissen oder Synergien zwischen einzelnen Ökosystemdienstleistungen in verschiedenen Waldtypen (Kapitel VI).

Kapitel I gibt eine Einführung in das Thema Entwaldung, die Ursachen und die Auswirkungen auf die lokale Lebensgrundlage und die biologische Vielfalt mit besonderem Bezug auf den ghanaischen Regenwald, Darüber hinaus werden globale und nationale Initiativen vorgestellt, einschließlich der aktiven Wiederherstellung von Wäldern, um die Auswirkungen der tropischen Entwaldung umzukehren oder zu minimieren. Ferner werden in Kapitel I die Vorteile der Wiederherstellung für die lokalen Dorfgemeinschaften und die biologische Vielfalt erläutert, und in **Kapitel II** werden die methodischen Ansätze für die Erhebung von Ökosystemattributen vorgestellt.

In **Kapitel III** wurde neben den Bodeneigenschaften auch die unter- und oberirdische Biomasse von Bäumen in einem aktiven Bergbaufolgesanierungsgebiet untersucht. Die aufgenommenen Ökosystemattribute wurden mit den Werten in vier alternativen Landnutzungstypen verglichen, die einen Gradienten von einer nicht sanierten ehemaligen Bergbaustätte über ein landwirtschaftliches Feld bis hin zu einer agroforstlichen Plantage und einem natürlichen Wald als Referenz abdecken. Die charakteristischen Bodeneigenschaften des wiederhergestellten Waldes (RF) unterschieden sich nicht signifikant von denen des natürlichen Referenzwaldes (NF), mit Ausnahme der Schüttdichte (1,36 vs. 1,17 gcm⁻³) und der Basensättigung (92,26 vs. 95,19%), aber sie unterschieden sich signifikant von den Eigenschaften aller anderen Landnutzungstypen. Die Ergebnisse deuten auf eine erfolgreiche Wiederherstellung der Bodeneigenschaften 20 Jahre nach Beginn der Wiederherstellung hin. Die verbesserten Bodenbedingungen in dem wiederhergestellten Wald führten zur Entwicklung einer dichten Vegetationsdecke, welche die Kohlenstoffbindung durch die Zunahme der Biomasse über und unter dem Boden förderte.

In **Kapitel IV** wurde untersucht, ob die funktionale Struktur von Baumgemeinschaften die Bereitstellung von Ökosystemleistungen in verschiedenen Landnutzungstypen beeinflusst. Bei der funktionalen Zusammensetzung trennten sowohl das ökonomische Blattspektrum als auch die Samenmasse der auftretenden Bäume die verschiedenen Landnutzungstypen. Der Naturwald wurde von Pflanzenarten dominiert welche schnell Ressourcen akquirieren können, und der nicht natürliche Wald zeigte eine größere Variation im Funktionsraum (140,19 sd^3 für agroforstliche Pflanzungen und 109,40 sd^3 für wiederhergestellte Wälder im Vergleich zu 21,45 sd^3 im Naturwald). Die funktionelle Vielfalt der Baumgemeinschaften wurde am besten durch die Bodenbedingungen erklärt und stand in allen Waldtypen in einem positiven Zusammenhang mit der Bereitstellung von Ökosystemdienstleistungsschätzern und der Multifunktionalität von Baumgemeinschaften.

In **Kapitel V** wurde untersucht, wie sich die Wiederherstellung nach dem Bergbau auf die Arthropodengemeinschaften auswirkt im Vergleich zu einem natürlichen Referenzwald, zu alternativen Landnutzungsformen und zu einer nicht sanierten ehemaligen Mine. Die Gemeinschaften bodenaktiver Arthropoden unterschieden sich signifikant zwischen den Landnutzungstypen in Abhängigkeit von der Jahreszeit. Die Arthropodengemeinschaften des sanierten Waldes lag hinsichtlich ihrer taxonomischen Zusammensetzung zwischen der agroforstlichen Plantage und dem natürlichen Wald. Die nicht wiederhergestellte ehemalige Mine wies eine einzigartige und deutlich verarmte Gemeinschaftszusammensetzung im Vergleich zu den anderen Landnutzungstypen auf. Diese Unterschiede in den Arthropodengemeinschaften zwischen den Landnutzungstypen ließen sich am besten durch Vegetationsmerkmale erklären, vor allem durch die taxonomische Zusammensetzung und Vielfalt der Baumgemeinschaften und das Totholzvolumen.

Durch die Quantifizierung der verschiedenen Ökosystemattribute im Feld und ihre Umwandlung in Schätzwerte für Ökosystemleistungen wurden in erster Linie Synergien ohne offensichtliche negative Beziehungen zwischen den Ökosystemleistungen der verschiedenen Waldnutzungstypen festgestellt (**Kapitel**

VI). So nahm beispielsweise die Biomasse der Futterbäume gleichzeitig mit der Anzahl der streuzersetzenden Arthropoden zu, was auf eine synergetische Beziehung zwischen unterstützenden Ökosystemleistungen und der Bereitstellung von Nahrung hinweist. Außerdem nahm bspw die Biomasse der Futterbäume gleichzeitig mit der Anzahl der räuberischen Arthropoden zu.

Diese Arbeit trägt zu einem besseren Verständnis der Auswirkungen der aktiven Wiederherstellung von Bergbaufolgelandschaften auf die Beziehungen zwischen Boden- und Biodiversitätseigenschaften und deren Einfluss auf die Bereitstellung von Ökosystemdienstleistungen in einer wenig untersuchten Region bei, die von massiver Entwaldung betroffen ist. Die aktive Wiederherstellung, die vor 20 Jahren an einem ehemaligen Bergbaustandort durchgeführt wurde, hat ein Waldökosystem geschaffen, das dem natürlichen Referenzwald ähnlicher ist als anderen alternativen Landnutzungstypen im Untersuchungsgebiet. Es bleibt abzuwarten, wie sich dieses System in Zukunft verändern wird und ob die gleichzeitige Bereitstellung von hoher Bodenqualität, biologischer Vielfalt und Ökosystemdienstleistungen langfristig geleistet wird.

List of abbreviations

AFR100	African Forest Landscape Restoration Initiative
AF	Agroforestry plantation
AG	Agricultural field
C/N	Carbon Nitrogen ratio
dbh	Diameter at breast height
ES(s)	Ecosystem services
FAO	Food and Agricultural Organization
GS	Gravel site
MEA	Millennium Ecosystem Assessment
MSNW	Moist Semi-deciduous North West
NF	Natural forest
NMDS	Non-Metric Multidimensional Scaling Ordination
NPDP	National Plantation Development Programme
Phg	Plant Height
RF	Restored forest
SDMC	Stem Dry Matter Content
SER	Society for Ecological Restoration
Smass	Seed mass
SDVZ	Semi-Deciduous Vegetation Zone
SIMPER	Similarity Percentage Analysis
SLA	Specific leaf area

Chapter I: General Introduction

Deforestation continues to be one of the most pressing challenges for humanity, with effects manifested in loss of biological diversity, anthropogenic carbon emissions that drive global climate change, threatened food security issues and the destruction of local livelihoods (Hall et al., 2022; Acheampong et al., 2019; Giam, 2017; Grainger, 2008; Kindermann et al., 2008). Several factors, including land-use change (e.g., conversion of forests to agricultural land or urban settlements), mining, infrastructure development, logging, agricultural intensification, and wildfire, are the major drivers of deforestation worldwide (Szymański et al., 2021; Haywood & Henriot, 2019; Juárez-Orozco et al., 2017; Sonter et al., 2017). Deforestation continues at high rates, with over 420 million hectares of forest lost globally since 1990 and 10 million hectares lost yearly between 2015 and 2020 (FAO & UNEP, 2020). Tropical forests, including Ghana's rainforest, are severely threatened by deforestation, with the rate of destruction becoming more extreme over the past decades (Kyere-Boateng & Marek, 2021; Roberts et al., 2021; Zeppetello et al., 2020).

Over 794,214 hectares of forest cover were lost annually in Ghana between 2013 and 2015 (Ghana Forestry Commission, 2017). According to a recent report from the Global Forest Watch, over 1.1 Mha of forest was lost between 2001 and 2021, with adverse implications for biodiversity and local human communities. Primary causes are anthropogenically driven and usually linked to livelihood (e.g., agricultural expansion, hunting, artisanal mining, logging) and development (e.g., infrastructure projects; Bentsi-Enchill et al., 2022; Acheampong et al., 2019; Fagariba et al., 2018; Quacou, 2016). However, evidence of natural causes, including forest fires, plant diseases and pest infestation, also exists (Dahan & Kasei, 2022; Danquah, 2009).

Efforts to reduce the impacts of deforestation and mitigate consequences for local communities have revolved around global and local initiatives, including forest protection and policy interventions, payment for ecosystem service programs to compensate local people for conserving forests, and a series of afforestation and restoration programs (Amoah et al., 2022; Dampney et al., 2022;

Viszlai et al., 2016). All these efforts are linked to the global commitment to restoring 350 million hectares of degraded lands by 2030, which has been embraced by voluntary commitments from regional and national actors (IUCN, 2020). For instance, through the Forest Landscape Restoration Initiative (AFR100), Ghana is committed to restoring 2 million hectares of degraded lands by 2030 to enhance ecological integrity in degraded landscapes while improving local livelihoods (Foli, 2018).

Historical and current restoration efforts have focused on enhancing ecosystem functioning, reflecting the collective value of plants and animals and the effects these activities have on the physical and chemical conditions in these environments (Jax, 2005). For instance, the improvement of soil conditions to support plant growth that translates into appropriate habitat conditions for arthropods (e.g., spiders, insects) to survive and contribute to major ecosystem functions has been the focus of many restoration programs (Parkhurst et al., 2021; Lal, 2015). Other benefits are seen in the enhancement of the provision of ecosystem services such as food, timber provisioning, carbon sequestration and cultural services (Mosier et al., 2021). Restoration, hence, aims at enhancing biodiversity and thereby improving human livelihoods (Bullock et al., 2011).

Usually, a considerable amount of resources (e.g., money, time or labour) are invested into restoration programmes (Wainaina et al., 2020; De Groot et al., 2013) which requires a retrospective assessment of the success against a set of indicator attributes from undisturbed, but comparable ecosystems as a reference. In this study, we relied on a series of indicators classified as ecological (soil nutrients, carbon sequestration) and biodiversity components (tree species and functional diversity, structural attributes and the activity density of selected arthropod groups). To meet the reference system criteria for assessing ecological restoration projects (Hernandez-Santin et al., 2021; Pruitt et al., 2012; SER, 2004), we included the most dominant ecosystems in the area of the restored forest as reference systems for comparison of attributes. These include two forest reserves: a natural and undisturbed forest and an afforestation (agroforestry plantation) site. In addition to these two forests, agricultural fields reflecting the historical conditions

of the restored forest before it was mined were also included in the design. An unrestored former mining site was also added to the study design for comparison to unassisted succession development.

The co-occurrence of these surrounding land-use types and the restored area presents an ideal situation for comparing ecosystem attribute recovery 20 years after the start of active restoration. Therefore, this study aimed to investigate the effects of restoration activities that targeted vital ecosystem attributes in a restored former mining area with reference to the surrounding dominant land-use types. Specifically, I hypothesized that (i) the interventions applied to restore and manage a post-mining area improve ecosystem attributes (for example the soil status and tree diversity) beyond conditions observed in unrestored gravel mines or in alternative dominant land-use types (agricultural and agroforestry plantations) and even reaching levels comparable to a natural reference forest (Chapter III), (ii) soil conditions and the functional structure of tree communities drive ecosystem functions and multifunctionality in land-use types with trees, with the highest multifunctionality levels in the restored and natural forests (Chapter IV), (iii) the structure of tree communities coupled with pronounced climatic seasonality support a higher number of arthropods and arthropod functional groups, particularly in the wet season and in structurally heterogeneous land-use types (restored and natural forest) (Chapter V), and (iv) active forest restoration enhances the levels of ecosystem service provision similar to the reference forest, with possible trade-offs or synergies among individual ecosystem services across forest types (Chapter VI).

1.1 Deforestation and restoration in tropical forests

Tropical forests are incredibly diverse and serve as a habitat for large parts of the world's biodiversity (Pillay et al., 2022; FAO & UNEP, 2020; Brockerhoff et al., 2017; Giam, 2017). However, current estimates show that over 11.1 million hectares of forests were lost in the tropics in 2021 (Weisse & Goldman, 2022) due to human-mediated factors, including logging, agricultural expansion, mining, and wildfire (Kyere-Boateng & Marek, 2021; Acheampong et al., 2019; Giam, 2017).

Impacts are evident in the decreasing extent of tropical forest ecosystems, a reduction in biological diversity and ecosystem functioning, as well as in their ability to respond to disturbances (resistance and resilience) with serious implications for human livelihoods (McDonald et al., 2016; Lawrence & Vandecar, 2015).

Several restoration programmes have been initiated to stop the deforestation of tropical forests or minimize its impacts on local livelihoods and biodiversity and enhance the ecosystem service provisioning of such landscapes. One such program is the National Plantation Development Program (NPDP), which aims to develop a sustainable forest resource base for future resource demands while simultaneously enhancing environmental quality (Guuroh et al., 2021). In addition, at the local scale and as a corporate social responsibility, Newmont Ghana Gold Limited manages approximately 15.4 ha of a restored post-mining site to provide basic ecosystem goods and services to local human communities (Dampney et al., 2020).

1.2 Post-mining restoration

Mining, in all forms, has the tendency to destroy landscapes, including forests, as well as affect biodiversity detrimentally at multiple spatial scales (Sonter et al., 2018). To maximize the negative legacies, ecological restoration (either active or passive) is required to return a degraded ecosystem to recovery towards an appropriate reference ecosystem (Decleer & Bijlsma, 2021). Active restoration involves management techniques to eliminate the sources of disturbance while implementing strategies (e.g., tree planting) to accelerate recovery and overcome obstacles to recovery (Trujillo-Miranda et al., 2018; Holl & Aide, 2011). Passive restoration, however, involves eliminating environmental stressors (e.g., grazing, agricultural activities) for secondary succession to occur naturally (Morrison & Lindell, 2011).

Applying either passive or active restoration approaches depends on the resilience of the degraded ecosystem in question, the goal of a particular restoration project, the financial resources available and the land-use history (Díaz-García et al., 2020; Festin et al., 2019; Rohr et al., 2016; Holl & Aide, 2011).

Methods of restoration include physical (e.g., ploughing and addition of topsoil, biochar), chemical (addition of lime, fertilizer) and biological (use of green plants and associated microorganisms) methods (Festin et al., 2019; Lim et al., 2014). Restoration activities in this study included ploughing to level post-mining pits, followed by the addition of fertile topsoil, liming and planting tree species with predicted ecological and economic benefits.

1.3 The use of reference ecosystems in ecological restoration

Reference ecosystems are useful for evaluating restoration success in regard to a defined target, and they provide a basis for monitoring and assessing restoration outcomes (Durbecq et al., 2020; Stoddard et al., 2006). Thus, they act as a blueprint for evaluating whether a particular restoration program is developing along a satisfying trajectory that will lead to the recovery of desired ecosystem services (Pollock et al., 2012). They are usually remnant undisturbed natural areas with characteristics including well-developed biodiversity (local native plants, animals and other biota), without any threats, and in close proximity to the restored area under assessment (Decler & Bijlsma, 2021; SER, 2004).

In evaluating restoration projects, one could compare the attributes of the restored area (here restored forest) to such a positive target reference (pre-degraded state: here natural forest) and a negative reference (pre-restoration degraded state: here former mining site; Durbecq et al., 2020). To widen the scope of this comparison, we also included an alternative restoration approach (agroforestry plantation) and a dominant land-use type in the study region (agricultural fields; Figure 1).

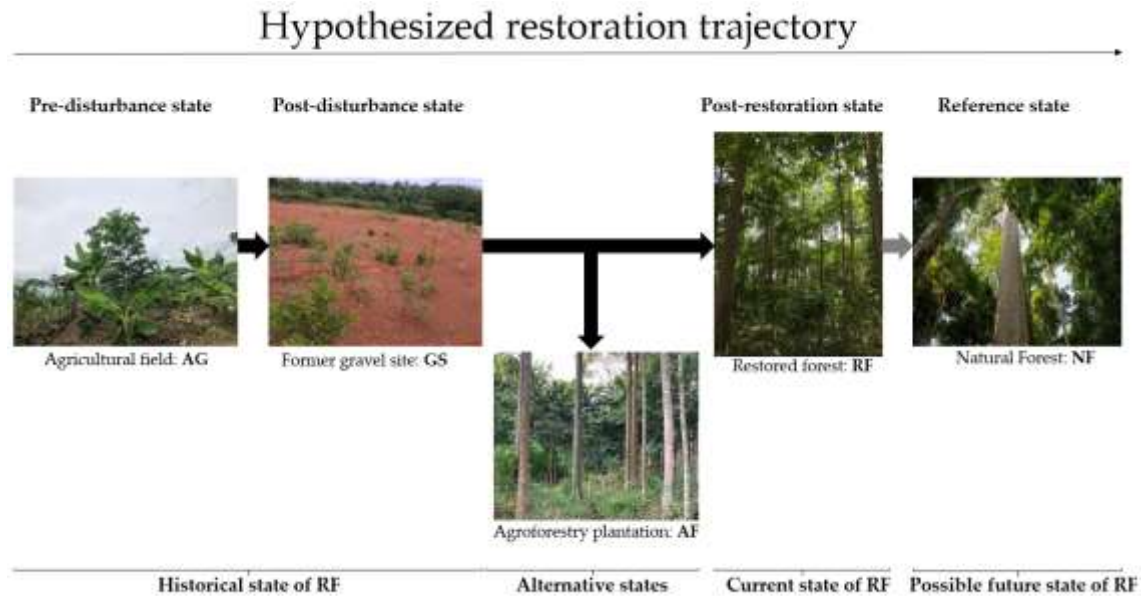


Figure 1: Land-use types studied for ecosystem attributes. Historical states and alternative trajectories are represented by the black arrows, and a potential future state is represented by a grey arrow

1.4 Evaluating restoration trajectories

According to the Society of Ecological Restoration (SER, 2004), a restored ecosystem should have enough biotic and abiotic resources to continue its development without further assistance. Such systems are characterized by attributes including the presence of assemblages of species (both plants and animals) similar to the reference ecosystem, the presence of indigenous species and functional groups essential for the stability of the restored ecosystem, suitable integration into a larger ecological matrix, the absence of potential threats, the ability to endure normal periodic stress events in the local environment and a self-sustaining system similar to the reference ecosystem (SER, 2004). There is, however, a high level of uncertainty about the effectiveness of restoration programs (Suding, 2011), which requires evaluation at different stages of a particular restoration program. Evaluating a restoration project at each stage of its trajectory allows for estimation of the level of success attained (Evangelista de

Oliveira et al., 2021). Such evaluation also allows tracking what works and what fails, thereby providing crucial information about best practices (Wortley et al., 2013).

To assess restoration outcomes, SER proposed nine key attributes categorized into three major ecosystem attributes, including vegetation structure, species diversity and ecological processes (Ruiz-Jaen & Mitchell Aide, 2005; SER, 2004). However, recognizing that restoration is a social entity, there has been a series of proposals to include socio-economic values and the effect on human well-being in restoration assessment (Wortley et al., 2013; Cardinale et al., 2012). Therefore, for this thesis, I utilized the framework mentioned above to evaluate restoration success, focusing on diversity (plant and arthropod richness and abundance), vegetation structure (vegetation cover, plant density and biomass) and ecological processes (nutrient cycling, herbivory, predation, carbon sequestration). Subsequently, I converted the measured attributes into ecosystem service proxies to quantify their potential effects on human well-being.

1.5 Effect of restoration on ecosystem service provisioning

ES(s), defined as the direct and indirect benefits people obtain from nature (Millennium Ecosystem Assessment, 2005; Daily, 1997), include provisioning (e.g., food, fodder, timber), regulating (e.g., climate, flood, disease regulation), cultural (e.g., aesthetic educational, recreational) and supporting services (e.g., soil formation, primary production, nutrient cycling; MEA 2005). Ecosystem transformation in times of global change coupled with an increasing human population is anticipated to reduce the ability of most ecosystems to offer goods and services to society (Gurgel et al., 2021; Guerry et al., 2015). An approach to promote the ability of ecosystems in terms of provisioning ecosystem services is restoration (Li et al., 2020; Alexander et al., 2016). Restoration, if successful, improves the flow of ecosystem services and biodiversity attributes (Bullock et al., 2011). Restoration projects aim at recovering processes (e.g., decomposition, fluxes of nutrients and energy, nutrient cycling), functions (e.g., regulatory, habitat, production functions) and the structure (e.g., the activities of producers,

consumers, decomposers, abiotic components) of an ecosystem (Palmer & Stewart, 2020; Gann et al., 2019).

1.6 Trade-offs, synergies and ecosystem restoration

The increasing demand for natural resources from a growing human population exerts intense pressure on ecosystem services provided by ecosystems (Howe et al., 2014). For this reason, most restoration projects aim at simultaneously maximizing the recovery of the provision of multiple ESs in a particular ecosystem and within a specific time frame. Depending on the type of restoration and the aim of a particular restoration program (hereafter referred to as the management choices), several interactions and feedback among different services could occur (Haase et al., 2012; Rodríguez et al., 2006).

The interactions among these services in an ecosystem could either be positive or negative (Birkhofer et al., 2015). A trade-off occurs when the increasing provision of one ES goes along with a decrease in another ES (Rodríguez et al., 2006). For instance, intensive forest management for timber production (timber products and economic returns) led to a decrease in cultural values as well as reduced biodiversity in southern Swedish oak forests (Löf et al., 2016). Similarly, among six ESs assessed based on proxies in Zimbabwe, Chawanji et al. (2018) observed that the provisioning of several services could not coexist on the same landscape without undermining the provision of others (e.g., a trade-off exists between cattle density and water supply and between grazing capacity and carbon sequestration). Several other pieces of evidence of trade-offs among different services have been observed worldwide (e.g., among regulating and provisioning services in cultural landscapes (Birkhofer, 2021; Birkhofer et al., 2018; Turner et al., 2014) and more diverse ecosystems (Raudsepp-Hearne et al., 2010).

Synergies between ES, on the other hand, occur when there is a simultaneous increase of more than one ES (e.g., the supply of one service leading to the supply of other services; Haase et al., 2012). Haase et al. (2012), for example, observed that forest restoration leads to simultaneous improvement in several cultural (e.g., recreational spaces), provisioning (e.g., food supply) and

regulating services (e.g., carbon storage).

Chapter II: General methodology

2.1 Study areas

This research was carried out in five distinct land-use types: 1.) an actively "restored forest" (Terchire restoration area; RF), 2.) an "agroforestry plantation" (Bosomkese forest reserve; AF), 3.) a "natural forest", (Asukese forest reserve; NF), 4.) an unrestored former "mining site" (Terchire abandoned gravel mine site; GS) and 5.) "agricultural fields" (surrounding arable lands; AG) are all located in the Tano North Municipal and Asutifi North political districts of the Ahafo and Bono regions within the Semi-Deciduous Vegetation Zone (SDVZ) of Ghana (Figure 1; Dampney et al., 2022). The zone has a mean daily temperature of 20°C and annual precipitation between 900 and 1500 mm (rainfall peaks between July and August). The soil classification according to the United States Department of Agriculture (USDA) Soil Taxonomy and the Food and Agriculture Organization (FAO) World Reference Base is Ultisols (Acrisols and Nitisols) on the uplands and Fluvents (Fluvisols) and Inceptisols (Cambisols) in the lowlands.

The Restored Forest (RF) lies at longitude 7°14.075' W, latitude 2°10.842' N and is located at Terchire in the Ahafo Region of Ghana. The RF site covers an area of about 15.4 hectares. It was previously gravel mined on the surface, and gravels from this area were used to construct the Sunyani-Kumasi highway (from 1994 to 1995). The area was then abandoned after mining until it was in 1999, subject to some earthworks (levelling and filling pits with mineral-rich topsoil) and active forest restoration by planting potted indigenous (e.g., *Celtis aldolfi-frider*, *Celtis zenkeri*, *Mangifera indica*, *Chrysophyllum albidum*, *Corynanthe pachyceras*, *Dichapetalum madagascariense*, *Pterygota macrocarpa*, *Ricinodendron heudelotii*, *Tetrapleura tetraptera* and *Sterculia Oblongata*) and fast-growing exotic nitrogen-fixing (e.g., *Leucaena leucocephala*, *Annona muricata*, *Terminalia catappa*, *Senna siamia*, *Tectona grandis*, *Cedrela odorata*) tree seedlings. A planting distance of 2 m × 2 m and a density of 1,111 seedlings per hectare were applied. Newmont Ghana Gold Limited currently manages RF intending to create an ecosystem that could mimic nearby natural managed forests in terms of

ecosystem goods and services provision.

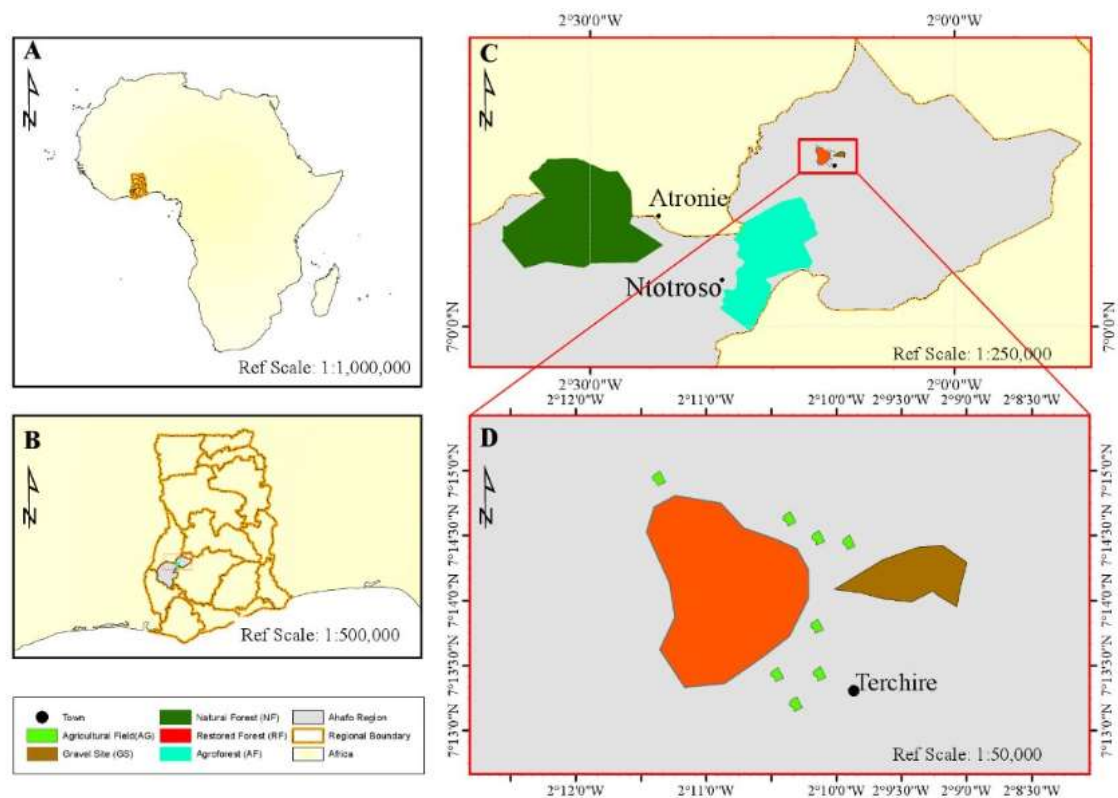


Figure 2: Map of Africa (A) showing Ghana with its regions (B), the Ahafo region with the two reference forests (C) and the restored forest and the historical land-use types (D)

The unrestored former mining site (GS) is 4 hectares in size and is located approximately 1.8 km from the RF site (Figure 2D), serving as a post-disturbance state reflecting the historical conditions of the RF site. The GS site lies at a longitude of $7^{\circ}14.150' W$ and a latitude of $2^{\circ}9.602' N$. It has been abandoned since 1995 and is currently experiencing massive soil erosion colonized by a few trees of *Anacardium occidentale*, or invasive species of *Chromolaena odorata* and *Pennisetum purpureum*.

The surrounding agricultural fields (AG; Figure 2D) in the vicinity of the RF site served as a pre-disturbance land-use reflecting the state of the current restored forest even before gravel mining. The AG site is cultivated with food crops such as maize, plantains, cassava, and cocoa and is occupied by a few remnant

tree species that are left on farms to provide shade for crops.

In addition, two managed forest reserves (Asukese Forest Reserve and Bosomkese Forest Reserve; Figure 2C) provide references (natural forest, NF) or alternative restoration approaches (agroforestry plantation, AF). Asukese Forest Reserve (NF) lies west of Sunyani – Mim highway through Atronie (About 19.3 km south-west of Sunyani). The NF site is located at a longitude of 2°31.107' W and latitude of 7°8.469' N, covers an area of about 26,936 hectares and is managed by the Sunyani Forest District. Three management zones are found within the NF site; the production zone (timber exploitation), degraded zone (under conversion and convalescence) and ecological zone (under protection; Ghana Forestry Commission, 2010). This study was carried out in the ecological sub-zone, which is protected with strong restrictions (limited access to people and resource extraction, except for domestic extraction and use of NTFPs) against anthropogenic activities (Ghana Forestry Commission, 2010). The NF site falls within the Moist Semi-deciduous North West (MSNW) vegetation zone (Hall & Swaine, 1981). The zone has a structure consisting of three stories (upper, middle and lower canopies) with tall emergent trees reaching up to 60 meters high and characterized by the dominance of economic timber species, including *Triplochiton scleroxylon*, *Terminalia superba*, *Ceiba pentandra*, *Antiaris toxicaria*, *Pterygota macrocarpa*, and *Ricinodendron heudelotii* (Ghana Forestry Commission, 2010).

The Bosomkese Forest reserve (AF; Figure 2C) lies on longitude 2 °14.075' W, latitude 7°6.338' N, and is located within the Semi-deciduous South East vegetation zone (SSEZ), approximately 28 km east of Sunyani (Swaine, 1996). The AF site covers an area of about 14,580 hectares and is managed by the Bechem Forest District (Ghana Forestry Commission, 2013). Because of degradation emanating from encroachment for farming, wildfire, illegal logging etc., the area has been subjected to massive agroforestry interventions involving the inter-planting of trees (exotic and indigenous species) with annual and perennial food crops (e.g., plantain, maize, cassava) to supply food and energy needs as well as environmental benefits to forest fringe communities (Ghana Forestry Commission, 2013).

The AG and GS sites represent the historical state of the RF site, with the AF site representing the alternative trajectory and the NF site representing the “possible” future reference (Figure 1).

2.2 Sampling design

Eight plots (20 × 20 m at least 200 m apart) in each of the five land-use types resulting in 40 sampling plots were demarcated (systematically) to assess soil, biodiversity, forest and land-use attributes. The assessment focused on tree communities (diversity, composition, structure, functional traits), arthropod communities (activity density, family and functional composition), and ecological processes (soil physical and chemical properties, decomposition rate and carbon sequestration), which were later quantified into proxy-based ecosystem services (Figure 3).

The analyses in this study are based on various methods for the attributes in Figure 3. Plant attributes focused on tree communities and were only surveyed for the land-use types with trees (NF, AF and RF). The results are featured in Chapters III, IV, V and VI. Arthropod communities focused on the activity density and family composition of major arthropod groups surveyed at the NF, AF, RF and GS sites. The results are featured in Chapters IV, V and VI. Ecological processes focused on soil properties, decomposition rate and carbon sequestration, which were studied in all five land-use types (NF, AF, RF, AG and GS sites), and the results are featured in Chapters III, IV, and VI.

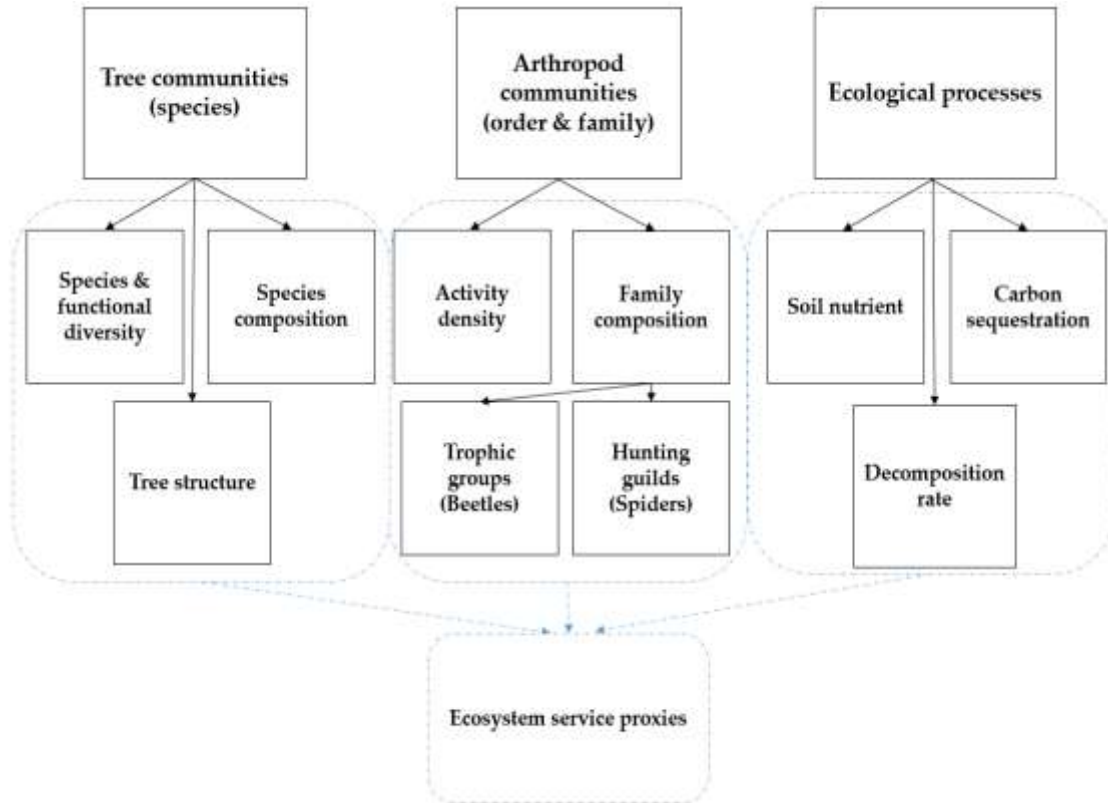


Figure 3: Flowchart showing the measured ecosystem attributes (top level), the major metrics in each attribute category (intermediate level) and their transformation into ecosystem service proxies (bottom level)

2.2.1 Sampling for soils

In each plot (8 plots in 5 land-use types), I sampled for soil properties by taking five soil cores (four from the corners and one from the centre) from a depth of 0-15 cm with a soil auger (diameter = 6.4 cm). The five samples were thoroughly mixed to form a single composite sample per plot which was later analysed in the laboratory for physical (texture: sand, silt and clay) and chemical (Phosphorus, Nitrogen, Sodium, C:N, pH, Cation Exchange Capacity, Soil Organic Matter, Base Saturation, and the Major cations: Calcium, Magnesium, Potassium) properties. In addition, three replicated undisturbed soil core samples were taken per plot with a metal ring (100 cm³) to analyse and calculate bulk density at the plot level.

2.2.2 Sampling for tree communities

In each plot, we counted and identified all trees with a diameter ≥ 10 cm at breast height (dbh). Trees were identified to species by a local botanist with the assistance of a field identification manual (Hawthorne & Gyakari, 2006). Tree diameter was measured with diameter tape, and tree height was estimated using a Nikon Forestry Pro-II Laser Rangefinder/Hypsometer (Nikon, USA) and specific wood density values obtained from the global wood density database (Zanne et al., 2009).

2.2.3 Sampling for plant traits

Plant traits such as the specific leaf area (SLA), leaf carbon and nitrogen ratio (C/N), isotopic carbon fraction ($\delta^{13}\text{C}$), stem dry matter content (SDMC), seed mass (S_{mass}) and plant height (Phg) were considered in this study. For each inventoried tree, 4 individuals (canopy trees with leaves exposed to the sun and no visible damage) of each species per forest type were selected. For each tree selected, 4 to 8 leaves and 4 stems (10 cm) were sampled and weighed for their fresh weight. The fresh leaves were then scanned and images were uploaded onto ImageJ software (Rueden et al., 2017) to calculate their SLA. Leaf and stem samples were dried at a constant temperature of about 70°C for 72 hours and later weighed for their dry weight. Seed mass values for each species were obtained from the TRY Plant Trait Database (Lewis et al., 2013) and the Royal Botanic Gardens (<https://data.kew.org/sid/>).

2.2.4 Sampling for arthropod communities

Arthropod sampling was carried out using a standardized trapping method involving the use of pitfall traps to sample and estimate the activity density of arthropods based on their locomotory activities (Perner & Schueler, 2004). Sampling was carried out in two seasons (dry: January to March and wet: June to August). For each plot, five pitfall traps were installed (4 at the corners and 1 at the centre), filled with propylene glycol mixed with water (50:50%), and covered with

a selective wire grid to avoid litter-fall and to minimise by-catch (e.g., rats). Traps were further sheltered with a small roof to avoid dilution of the trapping solvent by water (Underwood & Quinn, 2010). Traps were emptied weekly for 10 weeks in each sampling season and stored in 70% ethanol.

2.2.5 Proxy-based ecosystem service quantification

The proxy-based ecosystem services considered in this study include provisioning (food, fodder, medicine, mulch tree biomass), regulating (predator numbers, carbon storage), supporting (decomposer numbers, nutrient cycling) and cultural (tree richness) services.

Inventoried tree species were classified into providers of tree-related ES (food, fodder, fuelwood, medicine or mulch trees) based on the Useful Tropical Plants Database; Fern et al., 2014), and their biomass was calculated from an improved allometric equation for the pantropical region ($\ln(\text{AGB}) = \alpha + \beta \ln(p \times D^2 \times H) + \varepsilon$; Chave et al., 2014) based on tree dbh, estimated height, and specific wood density values of trees. The carbon stock for each tree was estimated by assuming 50% of each tree's biomass (Lewis et al., 2013). Arthropods were identified to family and later grouped into major feeding guilds as proxies for decomposers and predators. The rate of decomposition (a proxy for nutrient cycling) was estimated based on the tea bag index method (Keuskamp et al., 2013).

2.3 Chapter synthesis

To assess the state of ecosystem attributes in the restored forest, pre-restoration, alternative and reference land-use types, I carried out a systematic assessment of plant and arthropod communities, vegetation structure focusing on the vertical and horizontal orientation of trees, and ecological processes in five land-use types. Chapter I provides a basic overview of the ongoing deforestation, the causes and the consequences with particular reference to rainforest ecosystems in Ghana and further highlights global and national

strategies, including active forest restoration to minimize or stop deforestation. The benefits of restoration for local human communities and biodiversity are then discussed, followed by a generic overview of the study area, sampling design and data collection procedures (Chapter II). Afterwards, follows the various research chapters (Chapters III-VI) and the general discussion (Chapter VII) focusing on the aim and research hypotheses of this thesis.

The research chapters start with an investigation into how the soil conditions of a former gravel mining area have improved by restoration activities (Chapter III) to support plant growth (Chapter IV), which then provides essential resources (e.g., food and habitat) for arthropods (Chapter V). Ultimately, ecosystem service proxies quantified from soils (Chapter III), tree (Chapter IV) and arthropod (Chapter V) communities allow a holistic perspective of the success of restoration activities in terms of benefits for local human communities presented in Chapter VI (Figure 4).

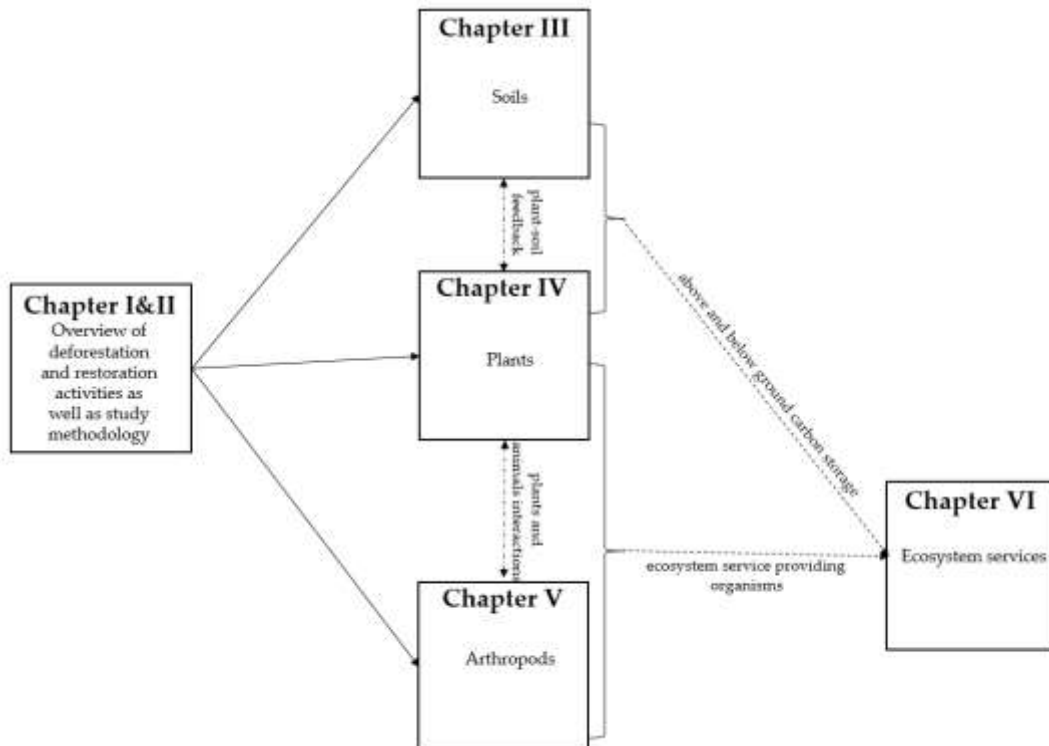


Figure 4: Synthesis of the four research chapters (III-VI) in this dissertation, their relationships and the introduction (Chapter I) and study site and design (Chapter II)

References

- Acheampong E, Macgregor C, Sloan S, Sayer J (2019) Deforestation is driven by agricultural expansion in Ghana's forest reserves. *Scientific African* 5: e00146. doi:10.1016/j.sciaf.2019.e00146.
- Alexander S, Aronson J, Whaley O, Lamb D (2016) The relationship between ecological restoration and the ecosystem services concept. *Ecology and Society* 21. doi:10.5751/es-08288-210134.
- Amoah A, Jumah A, Korle K (2022) Exploring willingness-to-pay for the restoration and maintenance of reserved forests in the Greater Accra Region of Ghana. *Forest Ecosystems* 9: 100041. doi:10.1016/j.fecs.2022.100041.
- Aronson J, Blatt C, Aronson T (2016) Restoring ecosystem health to improve human health and well-being: physicians and restoration ecologists unite in a common cause. *Ecology and Society* 21. doi:10.5751/es-08974-210439.
- Aronson J, Blatt C, Aronson T (2016) Restoring ecosystem health to improve human health and well-being: physicians and restoration ecologists unite in a common cause. *Ecology and Society* 21. doi:10.5751/es-08974-210439.
- Brockerhoff E, Barbaro L, Castagneyrol B, Forrester D, Gardiner B, González-Olabarria J, Lyver P, Meurisse N, Oxbrough A, Taki H, Thompson I, van der Plas F, Jactel H (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation* 26: 3005-3035. doi:10.1007/s10531-017-1453-2.
- Bullock J, Aronson J, Newton A, Pywell R, Rey-Benayas J (2011) Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends in Ecology & Evolution* 26: 541-549. doi: 10.1016/j.tree.2011.06.011.
- Cardinale B, Duffy J, Gonzalez A, Hooper D, Perrings C, Venail P, Narwani A, Mace G, Tilman D, Wardle D, Kinzig A, Daily G, Loreau M, Grace J, Larigauderie A, Srivastava D, Naeem S (2012) Biodiversity loss and its impact on humanity. *Nature* 486: 59-67. doi:10.1038/nature11148.
- Chawanji S, Masocha M, Dube T (2018) Spatial assessment of ecosystem service trade-offs and synergies in Zimbabwe. *Transactions of the Royal Society of South Africa* 73: 172-179. doi:10.1080/0035919x.2018.1428235.

- Clarke, K. R., & Gorley, R. N. (2015). Getting started with PRIMER v7. *PRIMER-E: Plymouth, Plymouth Marine Laboratory*, 20(1).
- Dahan K, Kasei R (2022) Overview of Researches on Bush Fires for Natural Resources and Environmental Management in Ghana: A Review. *Environment and Natural Resources Research* 12: 48. doi:10.5539/enr.v12n1p48.
- Daily, G. C. (1997). Introduction: what are ecosystem services. *Nature's services: Societal dependence on natural ecosystems*, 1(1).
- Damptey F. G., Birkhofer K, Nsiah P, de la Riva E (2020) Soil Properties and Biomass Attributes in a Former Gravel Mine Area after Two Decades of Forest Restoration. *Land* 9: 209. doi:10.3390/land9060209.
- Damptey, F. G., Opuni-Frimpong, E., Nsor, C. A., Addai, J., Debrah, D. K., Schnerch, B., Bentsi-Enchill, F., & Henn, K. (2022a). Taxonomic and community composition of epigeal arthropods in monoculture and mixed tree species plantations in a deciduous forest of Ghana. *Journal of Forest Research*.
- Damptey F.G., Birkhofer K, Oliveras Menor I, de la Riva E (2022b) The Functional Structure of Tropical Plant Communities and Soil Properties Enhance Ecosystem Functioning and Multifunctionality in Different Ecosystems in Ghana. *Forests* 13: 297. doi:10.3390/f13020297.
- Damptey F. G., de la Riva E, Birkhofer K (2021) 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. *Frontiers in Forests and Global Change* 4. doi:10.3389/ffgc.2021.630959.
- Danquah, S. (2009, April). Deforestation as a result of wildfire incidence in the Worobong Forest Reserve in the Eastern Region of Ghana. In *EGU General Assembly Conference Abstracts* (p. 1544).
- De Groot, R. S., Blignaut, J., Van Der Ploeg, S., Aronson, J., Elmqvist, T., & Farley, J. (2013). Benefits of investing in ecosystem restoration. *Conservation Biology*, 27(6), 1286-1293. doi:10.1111/cobi.12158.

- Decler, K., & Bijlsma, R. J. (2021). Guidance and tools for effective restoration measures for species and habitats. In T. Van der Sluis & A. M. Schmidt (Eds.), *E-BIND Handbook (Part B): Scientific support for successful implementation of the Natura 2000 network*. (p. 20).
- Díaz, S., Lavorel, S., Chapin, F. S., Tecco, P. A., Gurvich, D. E., & Grigulis, K. (2007). Functional diversity—at the crossroads between ecosystem functioning and environmental filters. In *Terrestrial ecosystems in a changing world* (pp. 81-91). Springer, Berlin, Heidelberg.
- Dippenaar-Schoeman, A. S., & Jocqué, R. (1997). *African spiders: an identification manual* (Vol. 9). Pretoria: ARC-Plant Protection Research Institute.
- Durbecq A, Jaunatre R, Buisson E, Cluchier A, Bischoff A (2020) Identifying reference communities in ecological restoration: the use of environmental conditions driving vegetation composition. *Restoration Ecology* 28: 1445-1453. doi:10.1111/rec.13232.
- Edwards D, Socolar J, Mills S, Burivalova Z, Koh L, Wilcove D (2019) Conservation of Tropical Forests in the Anthropocene. *Current Biology* 29: R1008-R1020. doi: 10.1016/j.cub.2019.08.026.
- Evangelista de Oliveira R, Lex Engel V, de Paula Loiola P, Fernando Duarte de Moraes L, de Souza Vismara E (2021) Top 10 indicators for evaluating restoration trajectories in the Brazilian Atlantic Forest. *Ecological Indicators* 127: 107652. doi: 10.1016/j.ecolind.2021.107652.
- Fagariba C, Song S, Soule S (2018) Livelihood Economic Activities Causing Deforestation in Northern Ghana: Evidence of Sissala West District. *Open Journal of Ecology* 08: 57-74. doi:10.4236/oje.2018.81005.
- FAO, & UNEP. (2020). *The State of the World's Forests 2020*. FAO and UNEP. <https://doi.org/10.4060/ca8642en>
- Festin E, Tigabu M, Chileshe M, Syampungani S, Odén P (2018) Progresses in restoration of post-mining landscape in Africa. *Journal of Forestry Research* 30: 381-396. doi:10.1007/s11676-018-0621-x.
- Foli, E. G. (2018). *Reshaping the terrain; Forest landscape restoration efforts in Ghana* (p. 4) [GLF Factsheet]. CIFOR. globallandscapesforum.org

- Gann G, McDonald T, Walder B, Aronson J, Nelson C, Jonson J, Hallett J, Eisenberg C, Guariguata M, Liu J, Hua F, Echeverría C, Gonzales E, Shaw N, Decler K, Dixon K (2019) International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology* 27. doi:10.1111/rec.13035.
- Ghana Forestry Commission (2010) *Asukese Forest Reserve Management Plan*.
- Ghana Forestry Commission (2013) *Bosomkese Forest Reserve Management Plan*.
- Ghana Forestry Commission (2017) *Ghana's National Forest Reference Level*.
- Giam X (2017) Global biodiversity loss from tropical deforestation. *Proceedings of the National Academy of Sciences* 114: 5775-5777. doi:10.1073/pnas.1706264114.
- Grainger A (2008) Difficulties in tracking the long-term global trend in tropical forest area. *Proceedings of the National Academy of Sciences* 105: 818-823. doi:10.1073/pnas.0703015105.
- Guerry A, Polasky S, Lubchenco J, Chaplin-Kramer R, Daily G, Griffin R, Ruckelshaus M, Bateman I, Duraiappah A, Elmqvist T, Feldman M, Folke C, Hoekstra J, Kareiva P, Keeler B, Li S, McKenzie E, Ouyang Z, Reyers B, Ricketts T, Rockström J, Tallis H, Vira B (2015) Natural capital and ecosystem services informing decisions: From promise to practice. *Proceedings of the National Academy of Sciences* 112: 7348-7355. doi:10.1073/pnas.1503751112.
- Gurgel A, Reilly J, Blanc E (2021) Agriculture and forest land use change in the continental United States: Are there tipping points? *iScience* 24: 102772. doi: 10.1016/j.isci.2021.102772.
- Guuroh, R. T., Foli, E. G., Addo-Danso, S. D., Stanturf, J. A., Kleine, M., & Burns, J. (2021). Restoration of degraded forest reserves in Ghana. *Reforesta*, 12, 35–55.
- Haase D, Schwarz N, Strohbach M, Kroll F, Seppelt R (2012) Synergies, Trade-offs, and Losses of Ecosystem Services in Urban Regions: an Integrated Multiscale Framework Applied to the Leipzig-Halle Region, Germany.

- Ecology and Society 17. doi:10.5751/es-04853-170322.
- Hagan J, Vanschoenwinkel B, Gamfeldt L (2021) We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. *Ecology Letters* 24: 2537-2548. doi:10.1111/ele.13874.
- Hall C, Rasmussen L, Powell B, Dyngeland C, Jung S, Olesen R (2022) Deforestation reduces fruit and vegetable consumption in rural Tanzania. *Proceedings of the National Academy of Sciences* 119. doi:10.1073/pnas.2112063119.
- Hall, J. B., & Swaine, M. D. (1981). *Distribution and ecology of vascular plants in a tropical rain forest. Forest vegetation in Ghana*. Dr W. Junk Publishers.
- Haywood C, Henriot C (2019) Protecting Forests from Conversion: The Essential Role of Supply-Side National Laws. *Frontiers in Forests and Global Change* 2. doi:10.3389/ffgc.2019.00035.
- Hernandez-Santin L, Rudge M, Bartolo R, Whiteside T, Erskine P (2021) Reference site selection protocols for mine site ecosystem restoration. *Restoration Ecology* 29. doi:10.1111/rec.13278.
- Hooper D, Adair E, Cardinale B, Byrnes J, Hungate B, Matulich K, Gonzalez A, Duffy J, Gamfeldt L, O'Connor M (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486: 105-108. doi:10.1038/nature 11118.
- Howe C, Suich H, Vira B, Mace G (2014) Creating win-wins from trade-offs? Ecosystem services for human well-being: A meta-analysis of ecosystem service trade-offs and synergies in the real world. *Global Environmental Change* 28: 263-275. doi: 10.1016/j.gloenvcha.2014.07.005.
- Huang Y, Chen Y, Castro-Izaguirre N, Baruffol M, Brezzi M, Lang A, Li Y, Härdtle W, von Oheimb G, Yang X, Liu X, Pei K, Both S, Yang B, Eichenberg D, Assmann T, Bauhus J, Behrens T, Buscot F, Chen X, Chesters D, Ding B, Durka W, Erfmeier A, Fang J, Fischer M, Guo L, Guo D, Gutknecht J, He J, He C, Hector A, Hönig L, Hu R, Klein A, Kühn P, Liang Y, Li S, Michalski S, Scherer-Lorenzen M, Schmidt K, Scholten T, Schuldt A, Shi X, Tan M, Tang

- Z, Trogisch S, Wang Z, Welk E, Wirth C, Wubet T, Xiang W, Yu M, Yu X, Zhang J, Zhang S, Zhang N, Zhou H, Zhu C, Zhu L, Bruelheide H, Ma K, Niklaus P, Schmid B (2018) Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* 362: 80-83. doi:10.1126/science.aat6405.
- IUCN. (2020). *Restore our Future: The Bonn Challenge*. <https://www.bonnchallenge.org/>
- Jax K (2005) Function and “functioning” in ecology: what does it mean? *Oikos* 111: 641-648. doi:10.1111/j.1600-0706.2005.13851.x.
- Juárez-Orozco S, Siebe C, Fernández y Fernández D (2017) Causes and Effects of Forest Fires in Tropical Rainforests: A Bibliometric Approach. *Tropical Conservation Science* 10: 194008291773720. doi:10.1177/1940082917737207.
- Kindermann G, Obersteiner M, Sohngen B, Sathaye J, Andrasko K, Rametsteiner E, Schlamadinger B, Wunder S, Beach R (2008) Global cost estimates of reducing carbon emissions through avoided deforestation. *Proceedings of the National Academy of Sciences* 105: 10302-10307. doi:10.1073/pnas.0710616105.
- Kyere-Boateng R, Marek M (2021) Analysis of the Social-Ecological Causes of Deforestation and Forest Degradation in Ghana: Application of the DPSIR Framework. *Forests* 12: 409. doi:10.3390/f12040409.
- Lal R (2015) Restoring Soil Quality to Mitigate Soil Degradation. *Sustainability* 7: 5875-5895. doi:10.3390/su7055875.
- Lawrence D, Vandecar K (2015) Effects of tropical deforestation on climate and agriculture. *Nature Climate Change* 5: 27-36. doi:10.1038/nclimate2430.
- Li R, Zheng H, Polasky S, Hawthorne P, O'Connor P, Wang L, Li R, Xiao Y, Wu T, Ouyang Z (2020) Ecosystem restoration on Hainan Island: can we optimize for enhancing regulating services and poverty alleviation? *Environmental Research Letters* 15: 084039. doi:10.1088/1748-9326/ab8f5e.
- Lim K, Shukor M, Wasoh H (2014) Physical, Chemical, and Biological Methods for the Removal of Arsenic Compounds. *BioMed Research International* 2014:

- 1-9. doi:10.1155/2014/503784.
- Löf M, Brunet J, Filyushkina A, Lindbladh M, Skovsgaard J, Felton A (2016) Management of oak forests: striking a balance between timber production, biodiversity and cultural services. *International Journal of Biodiversity Science, Ecosystem Services & Management* 12: 59-73. doi:10.1080/21513732.2015.1120780.
- Loreau M (1998) Biodiversity and ecosystem functioning: A mechanistic model. *Proceedings of the National Academy of Sciences* 95: 5632-5636. doi:10.1073/pnas.95.10.5632.
- McDonald, T., Gann, G. D., Jonson, J., & Dixon, K. W. (2016). international standards for the practice of ecological restoration – including principles and key concepts. *Society for Ecological Restoration*, 48.
- Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: Synthesis*.
- Mosier S, Córdova S, Robertson G (2021) Restoring Soil Fertility on Degraded Lands to Meet Food, Fuel, and Climate Security Needs via Perennialization. *Frontiers in Sustainable Food Systems* 5. doi:10.3389/fsufs.2021.706142.
- Palmer M, Stewart G (2020) Ecosystem restoration is risky ... but we can change that. *One Earth* 3: 661-664. doi: 10.1016/j.oneear.2020.11.019.
- Parkhurst T, Prober S, Hobbs R, Standish R (2021) Global meta-analysis reveals incomplete recovery of soil conditions and invertebrate assemblages after ecological restoration in agricultural landscapes. *Journal of Applied Ecology* 59: 358-372. doi:10.1111/1365-2664.13852.
- Picker, M. (2012). *Field guide to insects of South Africa*. Penguin Random House.
- Pillay R, Venter M, Aragon-Osejo J, González-del-Pliego P, Hansen A, Watson J, Venter O (2022) Tropical forests are home to over half of the world's vertebrate species. *Frontiers in Ecology and the Environment* 20: 10-15. doi:10.1002/fee 2420.
- Pollock M, Beechie T, Imaki H (2012) Using reference conditions in ecosystem restoration: an example for riparian conifer forests in the Pacific Northwest. *Ecosphere* 3: art98. doi:10.1890/es12-00175.1.

- Pruitt, B. A., Miller, S. J., Theiling, C. H., & Fischenich, J. C. (2012). *The Use of Reference Ecosystems as a Basis for Assessing Restoration Benefits*. EBA Technical Notes Collection. ERDC TN-EMRRP-EBA-11. Vicksburg, MS: U.S. Army Engineer Research and Development Centre. <http://cw-environment.usace.army.mil/eba/>.
- Quacou I (2016) Unsustainable Management of Forests in Ghana from 1900-2010. *International Journal of Environmental Monitoring and Analysis* 4: 160. doi:10.11648/j.ijema.20160406.14.
- R Development Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. ISBN 3-900051-07-0.
- Raudsepp-Hearne C, Peterson G, Bennett E (2010) Ecosystem service bundles for analyzing trade-offs in diverse landscapes. *Proceedings of the National Academy of Sciences* 107: 5242-5247. doi:10.1073/pnas.0907284107.
- Roberts P, Hamilton R, Piperno D (2021) Tropical forests as key sites of the “Anthropocene”: Past and present perspectives. *Proceedings of the National Academy of Sciences* 118. doi:10.1073/pnas.2109243118.
- Rodríguez J, Beard, Jr. T, Bennett E, Cumming G, Cork S, Agard J, Dobson A, Peterson G (2006) Trade-offs across Space, Time, and Ecosystem Services. *Ecology and Society* 11. doi:10.5751/es-01667-110128.
- Rohr J, Farag A, Cadotte M, Clements W, Smith J, Ulrich C, Woods R (2016) Transforming ecosystems: When, where, and how to restore contaminated sites. *Integrated Environmental Assessment and Management* 12: 273-283. doi:10.1002/ieam.1668.
- Ruiz-Jaen M, Mitchell Aide T (2005) Restoration Success: How Is It Being Measured? *Restoration Ecology* 13: 569-577. doi:10.1111/j.1526-100x.2005.00072.x.
- SER. (2004). *The SER international primer on ecological restoration*. Society for Ecological Restoration International Science & Policy Working Group. <http://www.ser.org>
- Sonter L, Ali S, Watson J (2018) Mining and biodiversity: key issues and research needs in conservation science. *Proceedings of the Royal Society B*:

- Biological Sciences 285: 20181926. doi:10.1098/rspb.2018.1926.
- Sonter L, Herrera D, Barrett D, Galford G, Moran C, Soares-Filho B (2017) Mining drives extensive deforestation in the Brazilian Amazon. *Nature Communications* 8. doi:10.1038/s41467-017-00557-w.
- Stoddard J, Larsen D, Hawkins C, Johnson R, Norris R (2006) Setting expectations for the ecological condition of streams: the concept of reference condition. *Ecological Applications* 16: 1267-1276. doi:10.1890/1051-0761(2006)016[1267: seftec]2.0.co;2.
- Suding K (2011) Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. *Annual Review of Ecology, Evolution, and Systematics* 42: 465-487. doi:10.1146/annurev-ecolsys-102710-145115.
- Swaine M (1996) Rainfall and Soil Fertility as Factors Limiting Forest Species Distributions in Ghana. *The Journal of Ecology* 84: 419. doi:10.2307/2261203.
- Systat Software. (2010). *Sigma Plot version 12.0*. (Version 12) [Computer software].
- Szymański C, Tabeni S, Alvarez J, Campos C (2021) Diversity of plants and mammals as indicators of the effects of land management types in woodlands. *Forest Ecosystems* 8. doi:10.1186/s40663-021-00348-2.
- Tilman D, Lehman C, Thomson K (1997) Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Sciences* 94: 1857-1861. doi:10.1073/pnas.94.5.1857.
- Turner K, Odgaard M, Bøcher P, Dalgaard T, Svenning J (2014) Bundling ecosystem services in Denmark: Trade-offs and synergies in a cultural landscape. *Landscape and Urban Planning* 125: 89-104. doi: 10.1016/j.landurbplan.2014.02.007.
- Viszlai, I., Barredo, J. I., & San-Miguel-Ayanz, J. (2016). *Payments for Forest Ecosystem Services (SWOT Analysis and Possibilities for Implementation)* [JRC Technical Report].
- Wainaina P, Minang P, Gituku E, Duguma L (2020) Cost-Benefit Analysis of

Landscape Restoration: A Stocktake. *Land* 9: 465.
doi:10.3390/land9110465.

Weisse, M., & Goldman, L. (2022). *Forest Loss Remained Stubbornly High in 2021*. Global Forest Watch. <https://www.globalforestwatch.org/blog/data-and-research/global-tree-cover-loss-data-2021/>

Wortley L, Hero J, Howes M (2013) Evaluating Ecological Restoration Success: A Review of the Literature. *Restoration Ecology* 21: 537-543.
doi:10.1111/rec.12028.

Zeppetello V. L, Parsons L, Spector J, Naylor R, Battisti D, Masuda Y, Wolff N (2020) Large scale tropical deforestation drives extreme warming. *Environmental Research Letters* 15: 084012.
doi:10.1088/1748-9326/ab96d2.

Chapter III: Soil properties and biomass attributes in a former gravel mine area after two decades of forest restoration

Published: 26th June 2020 in **Land 2020**, 9, 209

[https:// doi:10.3390/land9060209](https://doi.org/10.3390/land9060209)

Frederick Gyasi Damphey^{1*}, Klaus Birkhofer¹, Paul Kofi Nsiah² and Enrique G. de la Riva¹

¹ Department of Ecology, Brandenburg University of Technology,
03046 Cottbus, Senftenberg, Germany

frederickGyasi.Damphey@b-tu.de (F.G.D.)

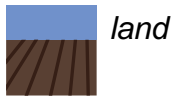
klaus.birkhofer@b-tu.de (K.B.)

enrique.garciadelariva@b-tu.de (E.G.d.I.R.)

² Department of Environmental Management, University of Energy and
Natural Resources, Sunyani 00233, Ghana

paul.nsiah@uenr.edu.gh (P.K.N.)

***Corresponding author**



Article

Soil Properties and Biomass Attributes in a Former Gravel Mine Area after Two Decades of Forest Restoration

Frederick Gyasi Damp¹, Klaus Birkhofer¹, Paul Kofi Nsiah² and Enrique G. de la Riva¹

¹ Department of Ecology, Brandenburg University of Technology, 03046 Cottbus, Senftenberg, Germany; Klaus.birkhofer@b-tu.de (K.B.); Enrique.garciadelariva@b-tu.de (E.G.d.I.R.)

² Department of Environmental Management, University of Energy and Natural Resources, Sunyani 00233, Ghana; Paul.nsiah@uenr.edu.gh

* Correspondence: FrederickGyasi.Damp¹@b-tu.de

Received: 3 June 2020; Accepted: 23 June 2020; Published: 26 June 2021

Abstract

The ongoing global deforestation resulting from anthropogenic activities such as unsustainable agriculture and surface mining threatens biodiversity and decreases both soil carbon and above-ground biomass stocks. In this study, we assessed soil properties and below- and above-ground biomass attributes in a restored former gravel mine area in Ghana two decades after active restoration with potted plants and fresh topsoil. We compared conditions to four alternative land-use types (unrestored abandoned gravel mine, agricultural field, agroforestry plantation, and natural forest) representing pre- and post-disturbance as well as natural reference states. We hypothesized that soil properties and related levels of below- and above-ground biomass in the restored forest share similarities with the natural reference systems and thereby are indicative of a trajectory towards successful restoration. Eight replicated subareas in each land-use type were assessed for a set of soil parameters as well as below- and above-ground biomass attributes. The soil properties characteristic for the restored forest differed significantly from pre-restoration stages, such as the abandoned gravel site, but did not differ significantly from properties in the natural forest (except for bulk density and base saturation). Above-ground biomass was lower in the restored area in comparison to the reference natural forests, while differences were not significant for below-ground biomass. Silt and effective cation exchange capacity were closely related to above-ground biomass, while below-ground biomass was related to soil organic carbon, bulk density, and potassium concentration in soils. Our results suggest that major steps towards successful restoration can be accomplished within a relatively short period, without the wholesale application of topsoil. Improving soil conditions is a vital tool for the successful development of extensive vegetation cover after surface mining, which also affects carbon sequestration by both above- and below-ground biomass. We emphasize that the use of reference systems provides critical information for the monitoring of ecosystem development towards an expected future state of the restored area.

Keywords: carbon sequestration; degradation; forest management; mining; restoration success

1 Introduction

The global reduction in forest cover following anthropogenic activities such as unsustainable agriculture, mining, and construction threatens biodiversity, alters soil properties, and decreases both soil carbon and above-ground biomass stocks [1–3]. Ecological restoration aims to enhance the ecological properties of an ecosystem that has previously been degraded, damaged, or destroyed to its pre-disturbance state [4]. Ecological restoration should also enhance the provision of ecosystem services from restored sites [5]. Degraded ecosystems, once restored, need to be monitored and assessed as such assessment will help to minimize problems resulting from the weak implementation of restoration activities [6]. That is, results from these assessments further help to advise decision-makers and land managers about future restoration activities and possible changes [7].

Evaluating the success of restoration projects has traditionally relied on descriptors of vegetation parameters [8,9]. However, there is a growing recognition that other descriptors, such as soil attributes, can give important additional insights into restoration success and associated levels of ecosystem services [10–12]. The ability of a particular soil to provide critical functions and ecosystem services (e.g., nutrient cycling, carbon sequestration, production of food, or physical stability) is usually assessed when evaluating restoration projects [13,14]. For example, levels of soil organic carbon, total nitrogen, and available potassium play an essential role in maintaining soil quality and fertility status [15,16] as well as vegetation recovery [17]. Nitrogen is an essential nutrient for plant growth, while soil texture correlates with hydrological processes such as run-off, infiltration rate and water holding capacity (e.g., [18]). Thus, the development of soil properties at restoration sites has profound effects on the structure and functioning of the ecosystem [17,19]. Restoration activities hold the potential to enhance soil conditions by retaining

and supplying nutrients to plants [20], creating a positive soil carbon budget and ultimately increasing biodiversity through changes in soil properties [21]. Vegetation benefits from physical support and other essential soil physical properties while soils benefit from vegetation-related functions such as nutrient cycling or erosion control [22–24]. These feedbacks link vegetation properties tightly to soil development, and vice versa, often resulting in a positive plant–soil feedback loop [25]. Tropical forests and their biodiversity are facing persistent threats due to deforestation and forest alterations [2]. The high forests of Ghana have lost about 4.9 million hectares (as of 2010), with an annual deforestation rate of approximately 2 % [26]. This loss is mainly caused by anthropogenic factors (e.g., logging, farming, mining, and construction) and wildfires [27–29] and has motivated the implementation of restoration projects in the last few decades.

In this study, we aim at assessing the recovery of ecosystem functions and services in a restored area by comparing the status of its soil properties and below- and above-ground biomass attributes with four different alternative land-use types from surrounding areas: (I) a former gravel mine without human intervention for the last 20 years; (II) smallholder agricultural fields representing the historic pre-mining conditions in some sections of the restored forest; (III) agroforestry plantation (Bosomkese Forest Reserve), which has been subjected to illegal logging, encroachment for farming, and wildfires as well as afforestation interventions; and (IV) natural forest (Asukese Forest Reserve), which has been under strict protection for the last 86 years. Although reference ecosystems may offer an important baseline for restoration projects, since they represent a pre-disturbance state of an ecosystem [30], few studies have addressed this question experimentally using comparative analyses (e.g., [31]), and, to our knowledge, no studies have addressed whether the soil attributes and their associated carbon stock evolve after restoration with regard to alternative land-use types in a tropical forest. The co-occurrence of these alternative land-use types and the restored area at relatively small spatial scales offer ideal conditions to compare soil properties and below- and above-ground biomass to understand the outcome of restoration activities 20 years

after their implementation. Under this framework and based on previous studies in tropical regions of Africa, we hypothesized that the intervention adopted by Newmont Gold Ghana Limited to restore and manage a formally abandoned gravel mine area has improved soil conditions and vegetation development towards levels observed in the agroforestry plantation and natural forest ecosystems in the study area. We further hypothesized that the observed levels of soil properties have a significant positive influence on carbon sequestration and that we expect to find strong correlations between soil properties and attributes related to carbon sequestration (e.g., organic root carbon and above-ground biomass).

2. Materials and Methods

2.1. Study Area

The following land-use types were selected, each with eight replicated study plots for a system comparison: unrestored gravel mine site (GS) as a post-disturbance state, agricultural field (AG) as pre-disturbance state, agroforestry plantation (AF) as alternate trajectory, and natural forest (NF) as reference state and restored forest (RF) (Figure 1).

The RF covers an area of 15.4 ha and is located at Terchire in the Ahafo Region of Ghana (longitude 7°14.075' N, latitude 2°10.842' W). The GS covers an area of about 4 ha and is located 1.8 kilometres from the RF (longitude 7°14.150' N, latitude 2°9.602' W). The GS has been abandoned since 1995 and colonized by few *Chromolaena odorata* and *Pennisetum purpureum*. The AGs are located in the surrounding areas of the RF and are cultivated with maize, plantain, cassava, cocoa, among others. Two managed forests reserves, the Asukese Forest Reserve (natural forest, NF) and the Bosomkese Forest Reserves (agroforestry plantation, AF), were included as forest reference systems in the study area. The NF is located in the moist semi-deciduous north-west forest zone (latitude 7°8.469' N, longitude 2°31.107' W).

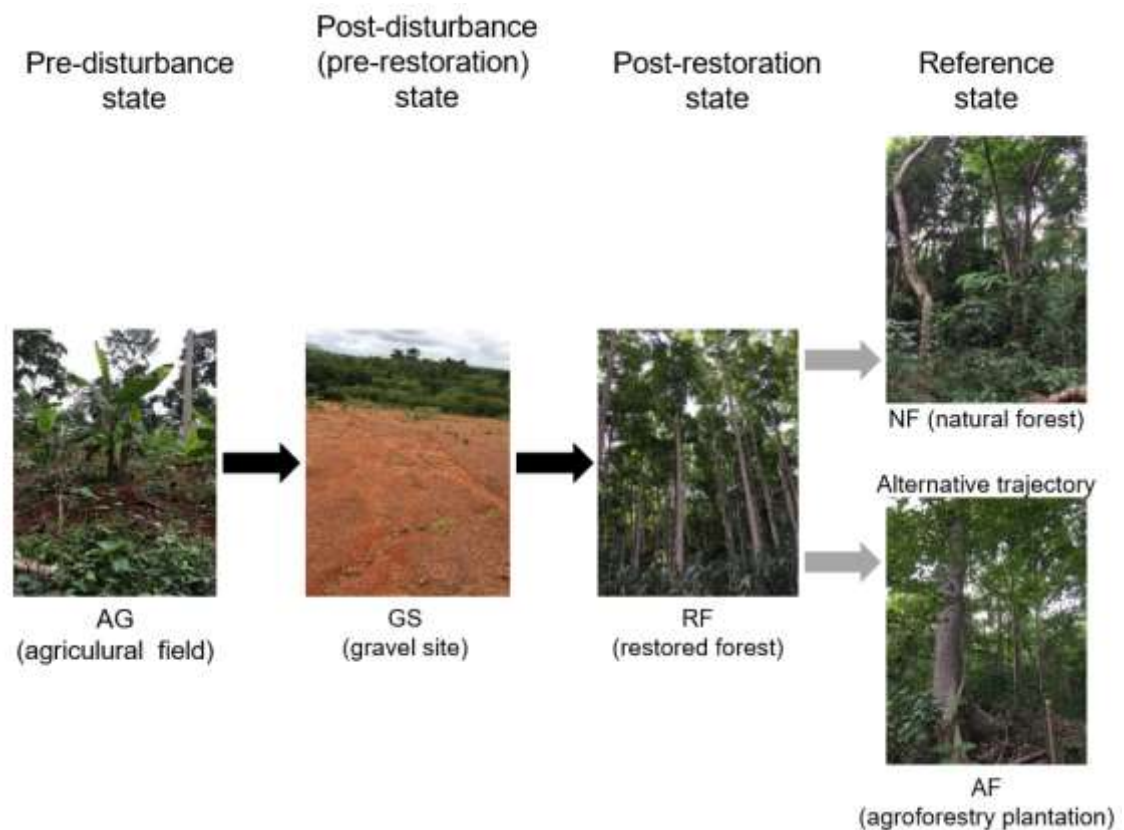


Figure 1. Known previous (black arrows) and potential future (grey arrows) state transitions of the restored forest over time. AG: agricultural field, GS: abandoned gravel-mined site, RF: restored forest, AF: agroforestry plantation, and NF: natural forest.

The AF is located in the semi-deciduous south-east forest zone (latitude $7^{\circ}6.338' N$, longitude $2^{\circ}14.782' W$). The soils of the five land-use types are classified according to the United States Department of Agriculture (USDA) Soil Taxonomy and the Food and Agriculture Organization (FAO) World Reference Base as Ultisols (Acrisols and Nitisols) on the uplands and Fluvents (Fluvisols) and Inceptisols (Cambisols) in the lowlands [32]. Climatic conditions are very similar for all the five land-use types because of their nearby geographic location (maximum distance between the study sites = 10.8 Km). Mean annual precipitation ranges between 900 to 1500 mm with two distinct seasons: a wet season (April–October) and a dry season (November–

March). The mean daily temperature in the study region is 25°C [29].

At the time of mining operations at the GS (from 1994 to 1995), the topsoil was stripped but was not stockpiled. The subsoil was removed for road construction, leaving the area severely degraded and open. To initiate and assist the recovery of the degraded condition, fertile soil was brought from elsewhere to fill the mine-out pits, followed by the planting of potted seedlings of some selected tree species in 1999. Both indigenous and fast growing exotic nitrogen fixing trees (e.g., *Leucaena leucocephala*) were planted at a planting distance of 2 × 2 m and a density of 1111 seedlings per each hectare. In 2000, NGGL started to manage the planted trees to create an ecosystem that could be capable of providing basic ecosystem goods and services to society.

2.2. Sampling Design

In each of the five land-use types under assessment, eight plots with sizes of 20 × 20 m were demarcated for sampling. All trees with a diameter ≥ 10 cm at breast height (dbh) were identified to species level and counted with the assistance of a local botanist and a field manual [33] in the RF, NF, and AF plots (the GS and AG plots did not have trees; hence, they were excluded for this measurement). The dbh of all stands was measured with a Vernier calliper, and individual tree height was estimated based on trigonometric calculations [34]. Above-ground biomass (AGB) for individual trees was determined using the measured dbh, the height, and wood density values obtained from the global wood density database [35] based on an improved allometric equation for the pantropical regions [36]. Roots were sampled using the soil core method [37] at a depth of 30 cm. Sampling for soil parameters was based on five replicated samples (four from each corner and one at the centre) in each plot with a soil auger (diameter = 6.4 cm). All replicated samples from the same plot were then pooled and thoroughly mixed to form a single composite sample, which was later analysed for chemical properties. Three replicated undisturbed soil cores for each plot were collected with a 100 cm³ metal ring and further analysed in the laboratory for bulk density.

2.3. Laboratory Analyses of Soil and Root Samples

Except for the determination of bulk density, soil samples used for the determination of all other parameters were air-dried, crushed, and sieved through a 2 mm mesh. The recipient sample (< 2 mm) was analysed for pH, soil organic matter/soil organic carbon (SOM/SOC; %), N (%), P (mg kg^{-1}), Na (Cmol kg^{-1}), K (Cmol kg^{-1}), Mg (Cmol kg^{-1}), Ca (Cmolc kg^{-1}), H (Cmolc kg^{-1}), and Al (Cmolc kg^{-1}) concentrations as well as particle size distribution. Soil pH was electrochemically determined using a multi-parameter PC 300 series electrode at a ratio of 5:1 soil to water suspension [38]. Organic matter was estimated by the loss of weight on ignition method using a muffle furnace model L9/S, at 550 °C for four hours, whereas total nitrogen concentration was determined by the Kjeldahl method [38].

Total phosphorus (P) was measured by the blue complex molybdate and thiophosphate method in acid solution and analysed using the Buck Scientific Spectrophotometer (BSS) model 280 G. The volumetric sodium tetraphenyl boron method was employed in estimating exchangeable Na and K, after dry ash digestion, and analysed with a Jenway flame photometer model PFP7, while Mg and Ca were determined with the aid of a Spectrophotometer (BSS 280 G), after extraction by ammonium acetate [38]. Exchangeable acidity due to hydrogen (H) and aluminium (Al) was extracted using a 0.1N KCl solution and the filtrate titrated with 0.05N NaOH to a colourless endpoint. Exchangeable acidity (Al and H) was determined by adding 4ml of 3N to the extract and titrated with 0.05N HCl to a pink endpoint. The effective cation exchange capacity (ECEC) was estimated through the summation of base cations (Na, K, Mg, and Ca) and acidic cations (H and Al), while base saturation (BS) was calculated as a percentage of the base cations of ECEC [39].

For the physical parameters, bulk density (g cm^{-3}) was analysed by using undisturbed soil cores collected in a 100 cm^3 metal ring and weight determination after oven-drying [40]. The hydrometer method [41] was

employed for particle size analysis, and the textural class was determined through the textural triangle diagram according to the USDA soil texture classification system. Before analyzing root samples in the laboratory, samples were refrigerated at 4 °C for a week. Root biomass determination (%) followed the direct method [42].

2.4 Data Analysis

All plant biomass data were square-root transformed while data on soil properties were log-transformed ($\text{Log}(X + 1)$). Prior to transformation, data were normalized to improve the homogeneity of variances and to reduce any possible weight that may be due to differences in scale (units) as well as making the model more robust [43,44]. To minimize the issue of multiple testing of soil properties, a global analysis was first performed with permutational multivariate analysis of variance (PERMANOVA) [45] based on Euclidian distance of the normalized data. Univariate PERMANOVA models were used to analyse the data for below- and above-ground biomass. The models for soil properties and below-ground biomass used the factors “land-use type” with the five levels RF, GS, NF, AF, and AG and the eight individual study plots as replicates. The model for the above-ground biomass only used the levels RF, NF, and AF as GS and AG plots did not contain any trees. All analyses were based on unrestricted permutation of raw data and 9999 permutations. Bootstrap means for the multivariate soil property data in all land-use types were calculated to provide means and ellipses shown in a non-metric multi-dimensional scaling (n-MDS) ordination based on Euclidean distance [46]. The goodness of fit of the n-MDS ordination is reflected by its stress value [47]. Plymouth Routines in Multivariate Ecological Research (PRIMER 7 and the PERMANOVA add-on) [48] were used for these statistical analyses.

General linear mixed models (GLMMs) were used to test for an effect of soil properties on below-ground biomass. We used the factor “land-use type” as a random effect in these models. To avoid any bias induced by including highly correlated predictors [49], we excluded one variable from each

pair of variables with a correlation coefficient larger than 0.70 [50]. To avoid the overestimation of the models with spurious parameters with very poor weights on the models [51], we only fitted three-factor models in which the factors were added either additively or multiplicatively. We used the dredge function in the MuMIn package to generate the set of models based on maximum likelihood (ML) estimation and then ranked models following the Akaike information criterion corrected (AICc) for a small sample size [52]. We then calculated marginal R^2_m and conditional R^2_c [53] values. In the case of above-ground biomass, we did not use “land-use type” as a random factor as it only had three levels [49]. The relationship between environmental variables and above-ground biomass attributes was therefore assessed with a General Linear Model (GLM), using the factor “land-use type” as a block factor. Again, the best model was selected based on AICc, followed by post-hoc multiple pairwise comparisons (Tukey’s test) to test the differences between land-use types. The R software [54] was used for these statistical analyses.

3. Results

3.1. Physicochemical Soil Properties

In general, the soil properties of the RF showed similar values to the NF and AF, which suggested a positive development of soil properties as a result of the restoration interventions. Specifically, the RF showed similar pH, nitrogen (N), phosphorus (P), sodium (Na), calcium (Ca), magnesium (Mg), soil organic matter (SOM), effective cation exchange capacity (ECEC), and carbon to nitrogen ratio (C/N) to the NF and AF (Table 1). However, significant differences were observed for bulk density, showing higher values for the RF and lower values for GS. N, P, and K concentrations were extremely low for the GS in comparison to the RF. Except for the GS (which had a C/N ratio of 32, which is considered above the ideal threshold [25] for plant growth), all other land-use types were below this threshold, with the lowest C/N values in NF.

Table 1. Soil properties (mean and standard errors) of the five land-use types. Significant differences between sites were tested with PERMANOVA, and P-values are presented. Identical letters denote no significant differences between variables, while different letters denote significant differences between variables.

Properties	NF	AF	RF	AG	GS	Significance levels
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	
Sand (%)	62.14 ± 2.42	67.40 ± 2.32	61.62 ± 2.61	62.79 ± 1.66	61.49 ± 3.51	0.464
Clay (%)	15.13 ± 2.76	12.62 ± 2.70	16.63 ± 3.30	20.90 ± 3.12	21.17 ± 4.85	0.343
Silt (%)	22.74 ± 1.60	19.98 ± 2.45	21.75 ± 1.72	16.32 ± 1.82	17.35 ± 1.88	0.106
BD (gcm ⁻³)	1.17 ± 0.03c	1.28 ± 0.03b	1.36 ± 0.05ab	1.50 ± 0.06a	1.41 ± 0.08ab	0.001
pH	5.71 ± 0.18b	6.44 ± 0.19a	5.69 ± 0.14b	6.19 ± 0.12a	4.51 ± 0.10c	0.001
N (%)	0.29 ± 0.02a	0.19 ± 0.01b	0.22 ± 0.03ab	0.21 ± 0.01b	0.10 ± 0.01c	0.001
P (mgkg ⁻¹)	6.01 ± 0.52b	9.33 ± 2.93b	8.44 ± 2.29b	31.37 ± 12.17a	2.83 ± 0.30c	0.009
K (Cmol _c kg ⁻¹)	0.29 ± 0.02	0.22 ± 0.02	0.23 ± 0.05	0.26 ± 0.08	0.14 ± 0.00	0.195
Na (%)	0.18 ± 0.02a	0.14 ± 0.00a	0.17 ± 0.01a	0.18 ± 0.02a	0.11 ± 0.01b	0.007
Ca(Cmol _c kg ⁻¹)	10.85 ± 1.66a	12.91 ± 1.63a	9.48 ± 0.99a	11.09 ± 1.12a	5.48 ± 0.37b	0.003
Mg(Cmol _c kg ⁻¹)	3.43 ± 0.53a	5.33 ± 1.06a	4.24 ± 0.83a	2.58 ± 0.69ab	1.69 ± 0.17b	0.011
SOM (%)	7.98 ± 0.53a	7.04 ± 0.63a	8.80 ± 1.12a	8.50 ± 0.76a	4.55 ± 0.79b	0.004
ECEC Cmol _c kg ⁻¹)	15.45 ± 1.49a	19.23 ± 2.03a	15.32 ± 1.69a	14.81 ± 1.45ab	8.92 ± 0.34b	0.004
Base Saturation (%)	95.19 ± 0.88a	95.98 ± 1.38a	92.26 ± 0.85b	94.95 ± 0.65a	82.83 ± 2.06c	0.001
C/N	16.68 ± 1.84c	21.53 ± 1.69b	24.08 ± 3.27b	21.25 ± 1.69b	32.98 ± 7.21a	0.048

The calculated ECEC from the base cations (Na, K, Mg, and Ca) and acidic cations (H and Al) at the RF, NF, and AF had values above 15, and no significant difference was observed among these sites. The ECEC value of the RF was, however, significantly higher than both the GS and the AG. Base saturation was extremely high for all five sites (> 80 %) despite the exhibition of statistical differences. Soil pH was near neutral at AF and AG, slightly acidic at RF and NF, and acidic at the GS. In terms of physical parameters, the particle size distribution for all the sites exhibited relatively high sand contents (> 60 %) and low clay and silt contents, yielding texture of sandy - loam for RF, NF, and AF as well as AG, but sandy - clay loam for the GS.

PERMANOVA results showed significant differences in soil properties between the five land-use types (Sites - $F_{4,35} = 5.28$, $p < 0.001$). Pairwise comparison between the five land-use types further revealed significant differences between the NF and the AF ($p < 0.001$), the NF and AG ($p < 0.001$), the NF and the GS ($p < 0.001$), the AF and the AG ($p = 0.009$), the AF and the GS ($p < 0.001$), the RF and the GS ($P < 0.001$) and AG and the GS ($p < 0.001$). No statistically significant difference was, however, established between the NF and the RF, the AF and the RF, and the RF and the AG ($p > 0.05$). Distinct and well-defined groups (land-use types) based on soil properties were also displayed by the ordination of the bootstrap averages with a 2D stress value of 0.08. The GS is completely separated from the other land-use types, while a small marginal overlap is displayed between the NF and the RF. The three forest sites (NF, AF, and RF) are closely clustered away from the AG and the GS (Figure 2).

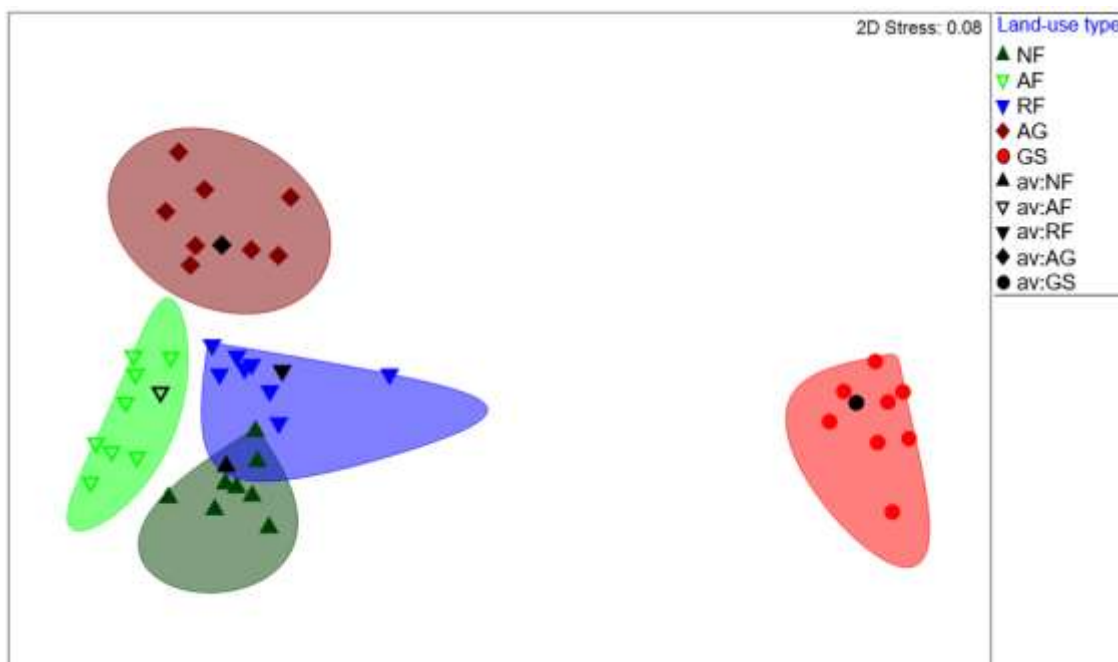


Figure 2. Non-metric multi-dimensional scaling (n-MDS) ordination showing resemblances between land-use types based on bootstrap average (av:) of soil properties with AG: agricultural field, GS: abandoned gravel-mined site, RF: restored forest, AF: agroforestry plantation, and NF: natural forest.

3.2. Species Composition and Abundance

n-MDS ordination revealed three distinct clusters when species composition among the three land-use types was compared with stress = 0.18 (Figure 3). Simper analysis confirmed mostly exotic tree species (*Leucaena leucocephala*, *Cassia siamea*) to be associated with RF, contributing about 30 % of the average similarity within the RF. Species composition for the AF consisted of both indigenous and exotic tree species (*Ceiba pentandra*, *Cedrela odorata*) while the NF was made up of only indigenous species.

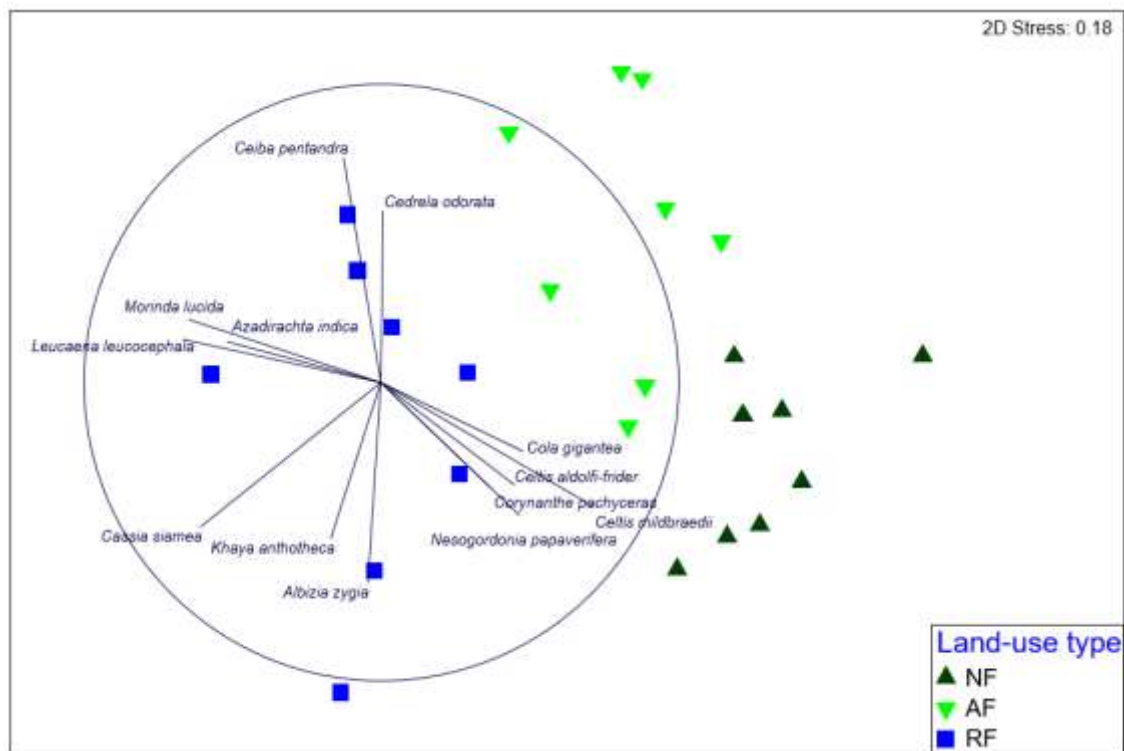


Figure 3. Non-metric multi-dimensional scaling (n-MDS) ordination of species composition among the three land-use types with trees (24 sample plots) with RF: restored forest, AF: agroforestry plantation, and NF: natural forest. The length and direction of vectors represent the strength and direction of the association between tree species and land-use types. The circle indicates a maximum vector length corresponding to a Pearson correlation coefficient of 1.0

3.3. Root Organic Carbon, Above-Ground Biomass, and Its Relationship to Soil Variables

The results of the GLMMs showed that an increase in organic root carbon was positively related to an increase in soil potassium and soil organic carbon and negatively related to bulk density (Figure 4).

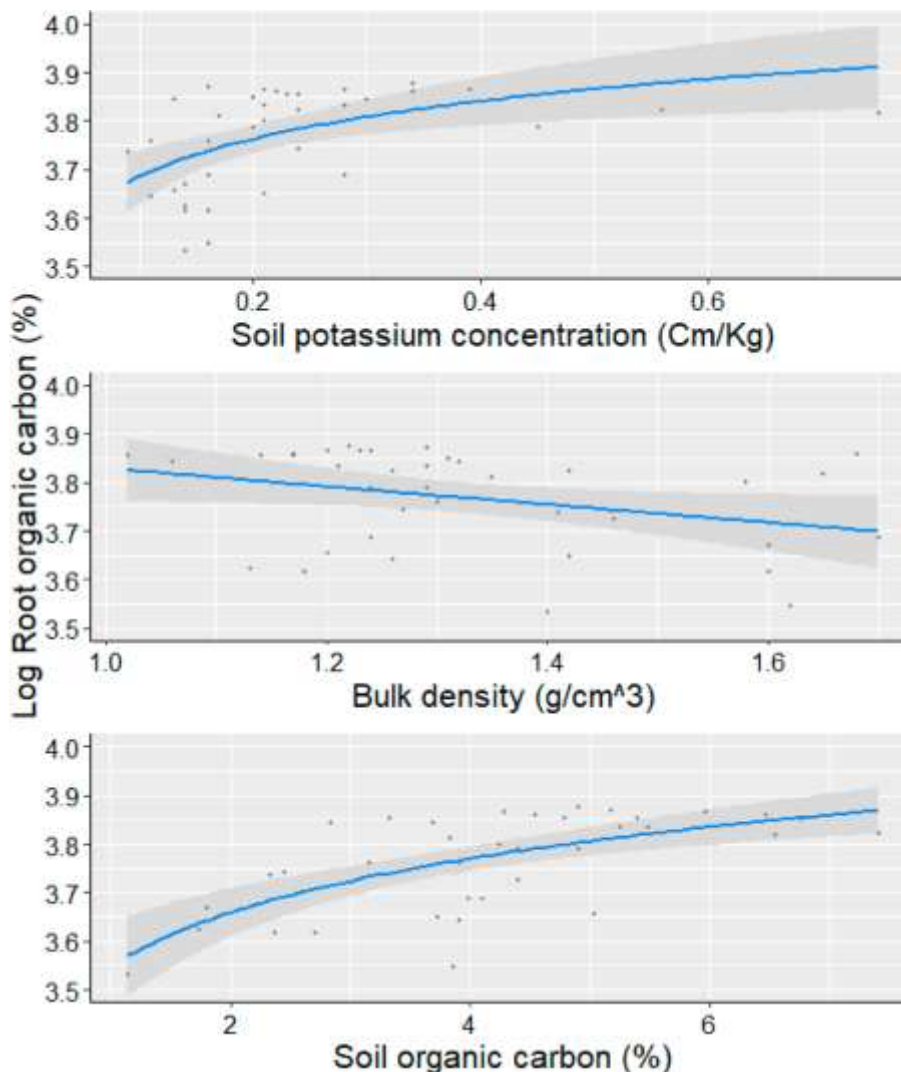


Figure 4. Significant relationship between organic root carbon and soil properties. The solid blue line represents the fitted relationship, and the grey area represents the 95% confidence interval.

The marginal R^2 of the model was 26 %, while the strong effect is related to the differences among sites (R^2 conditional = 62 %). Root organic carbon was highest in the NF (47 %), followed by the RF (46 %), the AF (43 %), the GS (38 %), and AG (38 %) (post-hoc Tukey's test; Figure 5A). The best model for the variation in AGB fits with silt and ECEC (R^2 =83 %). However, the highest proportion of the variance of this model was due to the effect of the block (the

differences among sites explained 50 % of the total variation). Thus, NF showed significantly higher values of AGB than RF (post-hoc Tukey's test; Figure 5B).

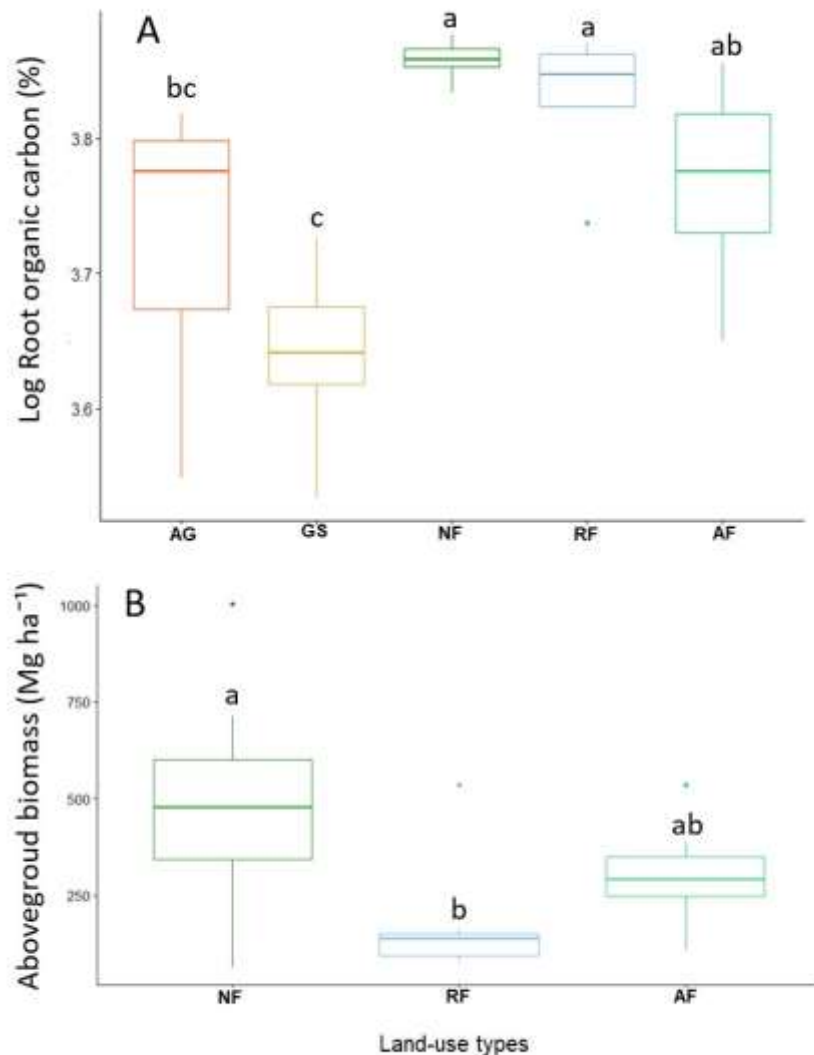


Figure 5. Box plot of organic root carbon (A) and above-ground biomass (B) between sites. The line represents the median value, the box limits are the 25th and 75th percentiles, error bars show 10th and 90th percentiles, and points show outliers. Different letters indicate significant differences between the land-use types (Tukey's test, $p < 0.05$).

ECEC played a secondary role, being negatively related to AGB, while AGB was

positively related to the increase of silt on RF and NF (Figure 6A & B).

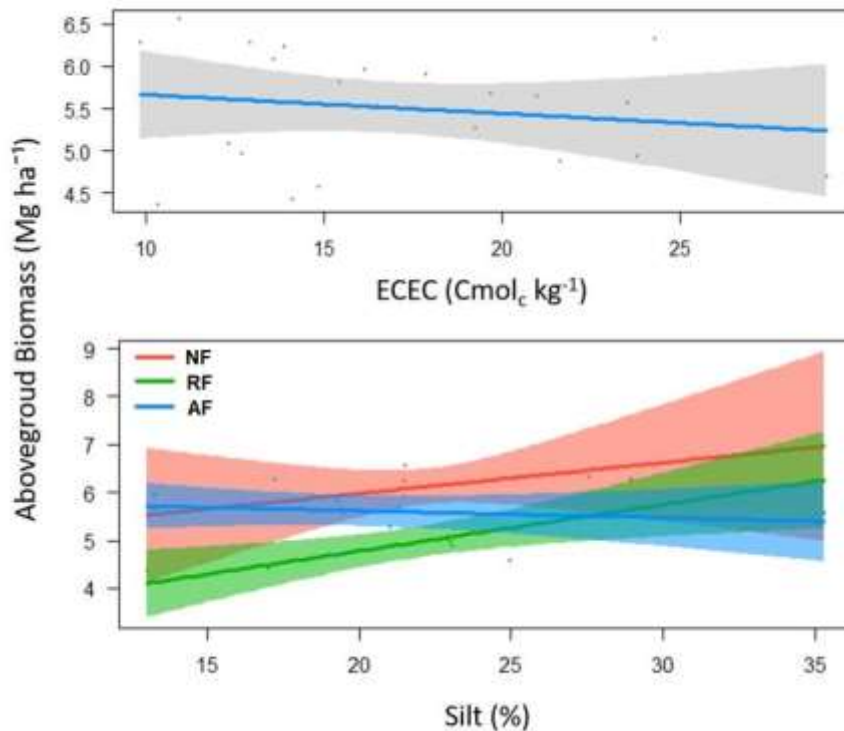


Figure 6 A & B: Relationship between above-ground biomass and significant soil attributes (ECEC and silt). The solid blue line represents the fitted relationship, and the grey area represents the 95 % confidence interval. ECEC: Effective cation exchange capacity.

4. Discussion

4.1. Influence of Restoration Interventions on Soil Attributes

Understanding the successful strategies on soil reclamation is an essential goal of restoration ecology [55,56]. Our results from the study area support our initial hypothesis that soil attributes have been improved over time compared to pre-disturbance and post-disturbance states. Soil properties in the restored forest differed significantly from these states but were not significantly different from natural forest 20 years after initiation of restoration (except for bulk density and base saturation). The restoration of post-mining sites by the establishment of

permanent tree cover is a useful practice for remediation [57]. However, one of the main challenges at the initial stages is the development of favourable conditions for plant growth in mining areas because of their highly disturbed character with high toxicity, compaction, and reduction of nutrients [58]. Therefore, the success of the restoration of mined areas depends on revegetation practices, especially during initial stages that are crucial for survival [57,59]. Two factors potentially contributed to the successful establishment of the vegetation in our study area: first, the management decision to initially use fast-growing exotic species that can tolerate the harsh initial environmental constraints [8] and have an ability to fix atmospheric nitrogen. For example, *Leucaena leucocephala*, which was very dominant in the restored forest, has been discussed extensively in the literature for its role in nitrogen fixation (e.g., [60,61]). *Cassia siamea* with its extensive root distribution also played a major role in erosion control and soil stabilization of the restored forest [62]. Second, seedlings of the planted tree species were potted using fresh topsoil.

The topsoil used for the potted seedlings seems to serve as suitable soil nuclei in providing the necessary nutrients and proper retention of these nutrients (high CEC and base saturation) for the young growing trees. This approach further ensured the emergence of other plant species from seeds stored in the topsoil [22]. Fresh topsoil has previously proven essential for successful vegetation establishment because of the provision of vital resources for plant growth, especially nutrients (N) and SOC [22,63]. Moreover, dispersed seeds from the nearby surrounding areas reaching these soil nuclei support effective vegetation establishment at the site. This is evident by the many plant species currently found at the restored forest, as compared to the lack of these species in the nearby abandoned and unrestored gravel mine site. The restored forest shows a significant improvement in soil pH with similar values for the reference forest sites, while the unrestored gravel site was strongly acidic with low nutrient concentration, which might explain its poor vegetation establishment. Soil pH is one the most important indicators for estimating soil health in former mine soils,

as a result of its influence on nutrient cycling and soil properties [64]. For instance, soil pH is primarily ascribed to the substantial increase in the basic cations (Na, K, Mg, and Ca), together with the corresponding reduction of exchangeable acidity (H and Al) [40,65]. Therefore, the significantly higher concentrations of SOC and total N at the restored forest compared with the abandoned gravel mine site could be ascribed to the restoration interventions that led to improved vegetation growth and development, which directly influenced SOC and N contents [40].

It is worth noting that previous studies have observed successful soil restoration of degraded mine sites after several decades [55,64,66]. Our results add to these studies by demonstrating that successful soil restoration could be obtained within two decades, at least in some tropical environments [56]. These results suggest that there is no universal global period for soil restoration, with significant differences depending on the specific context of each ecosystem, such as climatic conditions, surrounding vegetation, the origin of the disturbance, and the restoration approach [22,56,57,67]. Focusing on soil restoration, our results enable us to support afforestation after soil amendments as a critical catalyst for restoring soil properties after mining.

4.2. Carbon Sequestration and Biomass Reclaim

Forest functions as a terrestrial net sink in the global carbon cycle [68,69]. Our findings offer an insight into the potential impacts of restoration practices that aim at increasing plant biomass on C sequestration and the role of soil properties. Specifically, we show that middle-to-long term restoration practices increased biomass storage, but different patterns were observed for both the above- and below-ground components. We further show that active restoration practices (human intervention, initially planting trees in pots with topsoil) as opposed to passive restoration (unassisted recovery, sensu [70]) provide a more promising restoration approach after severe disturbance by surface mining. Although the restored forest area had a lower above-ground biomass compared to the natural forest and agroforestry plantation, similar root organic carbon concentration was

recorded across the three forest sites. The lower above-ground biomass stock recorded in the restored forest can be attributed to the higher number of trees with larger diameter in the natural forest [71–73]. Usually, mature forests are characterized by old trees with higher diameter; trees in younger stands on the contrary have smaller diameters in restored forest [74]. The lower above-ground biomass in the agroforestry plantation in comparison to the natural forest could be attributed mainly to anthropogenic disturbance such as logging and man-made wildfires in the area [28,29]. This highlights the impact that anthropogenic activity has on the functioning and service provision of forest ecosystems in the tropics. Root development and above-ground biomass are often positively related [75,76]. The restored forest shows similar root organic carbon concentration to the natural forest (in contrast to above-ground biomass), which suggests a faster recovery of below-ground than above-ground biomass. Roots constitute about 30% of the below-ground biomass with the highest production and turnover rates [77,78]. Studying the relationship between fine root biomass and vegetation recovery therefore seems crucial to better understanding long term carbon dynamics and storage patterns [77].

Relationships between above or below-ground biomass and soil properties have been previously addressed [79–81]. The lack of significant relationships between biomass and soil properties in this study may stem from threshold effects that could create nonlinearities between variables [82]. Although specific mechanisms are not evident from our study, the results suggest that biomass variability may be related to some soil parameters. The best model selected silt and ECEC as predictors of above-ground biomass across the three forest sites. Organic root carbon was related to soil organic carbon, bulk density, and soil potassium concentration. The relative proportions of sand, silt, and clay play a vital role for vegetation establishment in restored ecosystems, mainly due to their effects on moisture and nutrient retention as well as bulk density. Silt reduces the number of both macrospores and microspores in sand and clay by creating more mesospores that contain available water at field capacity, which is used by plants

for various physiochemical activities [40]. Consistent with our results, other studies also suggest that there is generally a decrease of exchangeable cations with the increase in clay on acid soils [83,84].

Concerning the organic root carbon, our results show positive feedback between root organic carbon and soil organic carbon. Most organic carbon in soils, such as organic and phenolic acids, are primarily plant-derived, being strongly determined by litter decomposition and root exudates [85]. Moreover, the improvement of the root system in restored areas has positive effects on nutrient cycling and C sequestration by promoting symbiotic association (i.e., mycorrhizas and N-fixing nodules), which together stimulates C sequestration by increasing the amount of C and nitrogen (N) entering soils [68,86]. Bulk density also accounts for the variations in root organic carbon among sites. Soil compaction strongly promotes water limitations and is known to drive seedling establishment in trees [87], potentially constraining plant root systems in mine soils [66]. The high bulk density in GS plots was due to the use of heavy machinery for mining, which caused soil compaction. Potassium is one of the essential elements for plants [88] and the positive relationship to below-ground biomass in this study is not surprising.

5. Conclusions

This study provides insights into the development of soil attributes and below- and above-ground biomass almost two decades after active forest restoration. Potted seedlings in fresh topsoil can serve as suitable soil nuclei in creating an optimal microclimate that overcomes potential limiting soil conditions at severely degraded mine sites. Our results suggest that major steps towards successful restoration can be accomplished within a relatively short period, without the wholesale application of topsoil. Improved soil conditions cause the development of extensive vegetation cover, which then influences carbon sequestration by both above- and below-ground biomass increases. By assessing restoration status compared to surrounding land-use types, we showed that the use of

reference systems provides critical information to judge the success of restoration approaches. Our findings improve the understanding of how an active restoration practice can mitigate the constraints inhibiting the recovery of former mining sites compared to pre- and post-disturbance, as well as natural reference states. However, communities with higher plant biomass will push themselves, in a positive plant–soil feedback loop, to an overall more fertile environment. This makes it challenging to infer the specific role of individual soil properties on the development of vegetation cover. Future monitoring of restoration trajectories in the study area should therefore focus on individual processes and mechanisms to which our study provides first insights.

Author Contributions: Conceptualization, F.G.D. and K.B. Data curation, F.G.D. Formal analysis, P.K.N. and E.G.d.I.R. Investigation, F.G.D. Methodology, F.G.D. and P.K.N. Project administration, F.G.D. and K.B. Resources, K.B. Software, E.G.d.I.R. Visualization, F.G.D. and E.G.d.I.R. Writing—original draft, F.G.D. Writing—review and editing, K.B and E.G.d.I.R. Supervision, KB and E.G.d.I.R. All authors have read and agreed to the published version of the manuscript.

Funding: FGD received much appreciated financial support from the Catholic Academic Exchange Service (KAAD). Open Access publication was supported by the Volkswagen Foundation (Az: 94646).

Acknowledgments: We are grateful to Newmont Gold Ghana Limited and Forest Service Division of Ghana for making the study sites available. We declare that no financial support was received from Newmont Gold Ghana Limited. We thank two anonymous referees and the editor for their comments on a previous version. Special thanks to PD Dr. Udo Bröring, Prof Dr. Manfred Wanner, and the entire staff at the Department of Ecology—Brandenburg University of Technology, Cottbus-Senftenberg for their support. We are also grateful to Daniel Debrah, Raymond Ayepah, Solomon Ankamah Danso, Pascal Agoro Prince, Napoleon Mensah, Kingsley Osei Bonsu, Gloria Djagbletey (Ph.D.), and Collins Ayine Nsor (Ph.D.) for their assistance.

Conflicts of Interest: The authors declare no conflict of interest

References

1. Pellikka, P.K.E.; Heikinheimo, V.; Hietanen, J.; Schäfer, E.; Siljander, M.; Heiskanen, J. Impact of land cover change on aboveground carbon stocks in Afromontane landscape in Kenya. *Appl. Geogr.* **2018**, *94*, 178–189. doi: 10.1016/j.apgeog.2018.03.017.
2. Giam, X. Global biodiversity loss from tropical deforestation. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 5775– 5777. doi:10.1073/pnas.1706264114.
3. Guo, X.; Meng, M.; Zhang, J.; Chen, H.Y.H. Vegetation change impacts on soil organic carbon chemical composition in subtropical forests. *Sci. Rep.* **2016**, *6*, 29607. doi:10.1038/srep29607.
4. Society for Ecological Restoration International Science & Policy Working Group. *The SER International Primer on Ecological Restoration*; Society for Ecological Restoration International: Washington, DC, USA 2004.
5. Bullock, J.M.; Aronson, J.; Newton, A.C.; Pywell, R.; Benayas, J.M.R. Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends Ecol. Evol.* **2011**, *26*, 541–549. doi: 10.1016/j.tree.2011.06.011.
6. Nilsson, C.; Aradottir, A.L.; Hagen, D.; Halld; Mitchell, R.J.; Raulund-Rasmussen, K.; Svavarsdóttir, K.; Tolvanen, A.; Wilson, S.D. Evaluating the process of ecological restoration. *Ecol. Soc.* **2016**, *21*, doi:10.5751/es-08289-210141.
7. IUCN, WRI. *A Guide to the Restoration Opportunities Assessment Methodology (ROAM): Assessing Forest Landscape Restoration Opportunities at the National or Sub-National Level*; Working Paper (Road-test edition). IUCN: Grand, Switzerland; 2014.
8. de la Riva, E.G.; Jimenez, M.D.; Mola, I.; Balaguer, L.; Costa-Tenorio, M.; Casado, M.A. Rates of local colonization and extinction reveal different plant community assembly mechanisms on road verges in central Spain. *J.*

- Veg. Sci.* **2011**, 22, 292–302. doi:10.1111/j.1654-1103.2010.01248. x.
9. Maestre, F.T.; Cortina, J.; Vallejo, V.R. Are Ecosystem Composition, Structure, and Functional Status Related to Restoration Success? A Test from Semiarid Mediterranean Steppes. *Restor. Ecol.* **2006**, 14, 258– 266. doi:10.1111/j.1526-100x.2006.00128. x.
 10. Magro, S.; López, M.G.; Casado, M.A.; Jiménez, M.D.; Trigo, D.; Mola, I.; Balaguer, L. Soil functionality at the roadside: Zooming in on a microarthropod community in an anthropogenic soil. *Ecol. Eng.* **2013**, 60, 81–87. doi: 10.1016/j.ecoleng.2013.07.061.
 11. Jimenez, M.D.; Mola, I.; Casado, M.A.; Balaguer, L.; Ruiz-Capillas, P.; Corona, M.E.P. SOIL Development at the Roadside: A Case Study of a Novel Ecosystem. *Land Degrad. Dev.* **2011**, 24, 564–574. doi:10.1002/ldr.1157.
 12. Harris, J. Soil Microbial Communities and Restoration Ecology: Facilitators or Followers? *Science* **2009**, 325, 573–574. doi:10.1126/science 1172975.
 13. Muñoz-Rojas, M. Soil quality indicators: critical tools in ecosystem restoration. *Curr. Opin. Environ. Sci. Heal.* **2018**, 5, 47–52. doi: 10.1016/j.coesh.2018.04.007.
 14. Greiner, L.; Keller, A.; Grêt-Regamey, A.; Papritz, A. Soil function assessment: review of methods for quantifying the contributions of soils to ecosystem services. *Land Use Policy* **2017**, 69, 224–237. doi: 10.1016/j.landusepol.2017.06.025.
 15. Maharjan, M. *Effect of Land Use on Soil Fertility and Carbon Sequestration*; Georg-August University of Göttingen: Göttingen, Germany, 2018.
 16. Laban, P.; Metternicht, G.; Davies, J. *Soil Biodiversity and Soil Organic Carbon: Keeping Drylands Alive*, 1st ed.; IUCN, International Union for Conservation of Nature, Gland, Switzerland, **2008**, Available from: <https://portals.iucn.org/library/node/47735> (accessed on 10 October 2019).
 17. Qiu, K.; Xie, Y.; Xu, N.; Pott, R. Ecosystem functions including soil organic carbon, total nitrogen and available potassium are crucial for vegetation

- recovery. *Sci. Rep.* **2018**, 8, 7607. doi:10.1038/s41598-018-25875-x.
18. Mendes, M.S.; Latawiec, A.E.; Sansevero, J.B.B.; Crouzeilles, R.; Moraes, L.F.D.; Castro, A.; Alves-Pinto, H.N.; Brancalion, P.H.S.; Rodrigues, R.R.; Chazdon, R.L.; et al. Look down-there is a gap-the need to include soil data in Atlantic Forest restoration. *Restor. Ecol.* **2018**, 27, 361–370. doi:10.1111/rec.12875.
19. Peng, X.; Horn, R.; Hallet, P. Soil structure and its functions in ecosystems: Phase matter & scale matter. *Soil Tillage Res.* **2015**, 146, 1–3. doi:10.1016/j.still.2014.10.017.
20. Shimamoto, C.Y.; Padiá, A.A.; Da Rosa, C.M.; Marques, M.C.M. Restoration of ecosystem services in tropical forests: A global meta-analysis. *PLoS ONE* **2018**, 13, e0208523. doi:10.1371/journal.pone.0208523.
21. Lal, R. Restoring Soil Quality to Mitigate Soil Degradation. *Sustainability* **2015**, 7, 5875–5895. doi:10.3390/su7055875.
22. Nsiah, P.K.; Schaaf, W. The potentials of biological geotextiles in erosion and sediment control during gold mine reclamation in Ghana. *J. Soils Sediments* **2018**, 19, 1995–2006. doi:10.1007/s11368-018-2217-7.
23. Gould, I.J.; Quinton, J.N.; Weigelt, A.; De Deyn, G.B.; Bardgett, R.D. Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecol. Lett.* **2016**, 19, 1140–1149. doi:10.1111/ele.12652.
24. Omoro, L.M.A.; Laiho, R.; Starr, M.; Pellikka, P.K. Relationships between native tree species and soil properties in the indigenous forest fragments of the Eastern Arc Mountains of the Taita Hills, Kenya. *For. Stud. China* **2011**, 13, 198–210. doi:10.1007/s11632-011-0303-7.
25. de la Riva, E.G.; Prieto, I.; Villar, R. The leaf economic spectrum drives leaf litter decomposition in Mediterranean forests. *Plant Soil* **2018**, 435, 353–366. doi:10.1007/s11104-018-3883-3.
26. FAO. Global Forest Resources Assessment, Main report: FAO Forestry Paper 163. FAO: Rome, Italy, 2010.

27. Acheampong, E.O.; MacGregor, C.J.; Sloan, S.; Sayer, J. Deforestation is driven by agricultural expansion in Ghana's forest reserves. *Sci. Afr.* **2019**, *5*. doi: 10.1016/j.sciaf. 2019.e00146.
28. Nindel, S. Forest Fire Dynamics and Carbon Stocks in Different Ecological Zones of Ghana; Technische Universität Dresden: Dresden, Germany, **2017**.
29. Addai, G.; Baidoo, P. The effects of forest destruction on the abundance, species richness and diversity of butterflies in the Bosomkese Forest Reserve, Brong Ahafo Region, Ghana. *J. Appl. Biosci.* 2013, *64*, 4763. doi:10.4314/jab.v64i1.88465.
30. Cash, R.N. A Reference for Restoration: Applying the Reference Site Model to Riparian Restoration Sites in the California Coastal Sage Scrub, Chaparral, and Oak Woodlands Ecoregion; Riparian Restoration, California, USA. 2013.
31. Ahirwal, J.; Maiti, S.K. Assessment of carbon sequestration potential of revegetated coal mine overburden dumps: A chronosequence study from dry tropical climate. *J. Environ. Manag.* **2017**, *201*, 369–377. doi: 10.1016/j.jenvman.2017.07.003.
32. NGGL. Newmont Ghana Gold Limited. In *Reclamation and Closure Plan Ahafo South Project*; 2015; P. 77.
33. Hawthorne, W.D.; Gyakari, N. Photo Guide for Forest Tree of Ghana. *A Tree Spotters Guide for Identification of Large Trees*; Oxford Forestry Institute: New York, UK, 2006;
34. Larjavaara, M.; Muller-Landau, H.C. Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. *Methods Ecol. Evol.* **2013**, *4*, 793–801. doi:10.1111/2041-210x.12071.
35. Zanne, A.M.; Lopez-Gonzalez, G.; Coomes, D.A.; Ilic, J.; Jansen, S.; Lewis, S.L. *Global Wood Density Database*; Dryad: Oakland, CA, USA, 2009.
36. Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M., Delitti, W., Duque, A., Eid, T., Fearnside, P., Goodman, R., Henry, M.,

- Martínez-Yrizar, A., Mugasha, W., Muller-Landau, H., Mencuccini, M., Nelson, B., Ngomanda, A., Nogueira, E., Ortiz-Malavassi, E., Péliissier, R., Ploton, P., Ryan, C., Saldarriaga, J. and Vieilledent, G. Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Boil.* **2014**, *20*, 3177–3190. doi:10.1111/gcb.12629.
37. Vogt, K.A.; Vogt, D.J.; Bloomfield, J. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant Soil* **1998**, *200*, 71–89. doi:10.1023/a:1004313515294.
38. Motsara, M.R.; Roy, R.N. *Guide to Laboratory Establishment for Plant Nutrient Analysis*; Food and Agriculture Organization of the United Nations: Rome, Italy, 2008; p.204.
39. Hazelton, P.; Murphy, B. Interpreting soil test results. In *What do All the Numbers Mean?* CSIRO Publishing, Clayton, Victoria, Australia. **2007**.
40. Weil, R.R.; Brady, N.C. *The Nature and Properties of Soils*. 5th ed.; Pearson: Columbus, OH, USA, **2008**; p. 1086
41. Bouyoucos, G.J. The Hydrometer as a New Method for the Mechanical Analysis of Soils. *Soil Sci.* **1927**, *23*, 343–354. doi:10.1097/00010694-192705000-00002.
42. Frasier, I.; Noellemeyer, E.; Fernández, R.; Quiroga, A. Direct field method for root biomass quantification in agroecosystems. *MethodsX* **2016**, *3*, 513–9. doi: 10.1016/j.mex.2016.08.002.
43. Harrison, X.A.; Donaldson, L.; Correa-Cano, M.E.; Evans, J.C.; Fisher, D.N.; Goodwin, C.E.; Robinson, B.; Hodgson, D.; Inger, R. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* **2018**, *6*, e4794. doi:10.7717/peerj.4794.
44. Zuur, A.F.; Ieno, E.N.; Elphick, C.S. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **2009**, *1*, 3–14. doi:10.1111/j.2041-210x.2009.00001.x.
45. Anderson, M.J.; Gorley, R.N.; Clarke, K.R. *PERMANOVA+ for PRIMER*:

- Guide to Software and Statistical Methods*. PRIMER-E. Plymouth: UK, 2008.
46. Oksanen, J.; Blanchet, F.G., Kindt, R.; Legendre, P.; Minchin, P.R.; O'hara R.B. *Package Vegan*; Communityecology package; 2013; Volume 9, pp. 1–295.
47. Clarke, K.R.; Gorley, R.N.; Somerfield, P.J.; Warwick, R.M. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 3rd ed.; PRIMER-E. Plymouth: UK, 014.
48. Clarke, K.R.; Gorley, R.N. *Getting Started with PRIMER v7*; PRIMER-E Ltd, Devon, UK:
49. Zuur, A.F.; Ieno, E.N.; Walker, N.; Saveliev, A.A.; Smith, G.M. Mixed effects models and extensions in ecology with R. *Stat. Biol. Health* **2009**, *32*, 574.
50. Luo, S., He, Y., Wang, Z., Duan, D., Zhang, J., Zhang, Y., Zhu, Y., Yu, J., Zhang, S., Xu, F., Sun, J., Han, Z. and Jiao, W., 2019. Comparison of the retrieving precision of potato leaf area index derived from several vegetation indices and spectral parameters of the continuum removal method. *European Journal of Remote Sensing*, *52*(1), pp.155-168. Comparison of the retrieving precision of potato leaf area index derived from several vegetation indices and spectral parameters of the continuum removal method. *Eur. J. Remote Sens.* **2019**, *52*, 155–168. doi:10.1080/22797254.2019.1572460.
51. Grueber, C.E.; Nakagawa, S.; Laws, R.J.; Jamieson, I.G. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Boil.* **2011**, *24*, 699–711. doi:10.1111/j.1420-9101.2010.02210. x.
52. Barton, A.D.; Ward, B.A.; Williams, R.G.; Follows, M.J. The impact of fine-scale turbulence on phytoplankton community structure. *Limnol. Oceanogr. Fluids Environ.* **2014**, *4*, 34–49. doi:10.1215/21573689- 2651533.
53. Nakagawa, S.; Schielzeth, H. A general and simple method for obtaining R^2 from generalized linear mixed effects models. *Methods Ecol. Evol.* **2012**, *4*, 133–142. doi:10.1111/j.2041-210x.2012.00261. x.

54. R Core Team. *R: A Language and Environment for Statistical Computing*. Vienna, Austria.
55. Wang, J.; Zhao, F.; Yang, J.; Li, X. Mining Site Reclamation Planning Based on Land Suitability Analysis and Ecosystem Services Evaluation: A Case Study in Liaoning Province, China. *Sustainability* **2017**, *9*, 890. doi:10.3390/su9060890.
56. Dutta, R.K.; Agrawal, M. Effect of tree plantations on the soil characteristics and microbial activity of coalmine spoil land. *Trop Ecol.* **2002**, *43*, 315–324.
57. Borišev, M.; Pajević, S.; Nikolić, N.; Pilipović, A.; Arsenov, D.; Župunski, M. Mine Site Restoration Using Silvicultural Approach. In *Bio-Geotechnologies for Mine Site Rehabilitation*; Elsevier: 2018; pp. 115–30. Available online: <https://linkinghub.elsevier.com/retrieve/pii/B9780128129869000075> (accessed on 10 October 2019).
58. Moreno-de las Heras, M. Development of soil physical structure and biological functionality in mining spoils affected by soil erosion in a Mediterranean-Continental environment. *Geoderma* **2009**, *149*, 249–56.
59. Nurtjahya, E.; Setiada, D.; Guhardja, E.; Muhadiono, Setiadi, Y. Revegetation of tin-mined land using various local tree species in Bangka island, Indonesia. *J. Am. Soc. Min. Reclam.* **2008** *1*, 14-19.
60. Chaer, G.M.; Resende, A.S.; Campello, E.F.C.; De Faria, S.M.; Boddey, R.M. Nitrogen-fixing legume tree species for the reclamation of severely degraded lands in Brazil. *Tree Physiol.* **2011**, *31*, 139–149. doi:10.1093/treephys/tpq116.
61. Bekunda, M. *Nitrogen Fixation in Leucaena Leucocephala and Effects of Pruning on Cereal Yield*; No. IAEA- TECDOC-1053, 1998.
62. Vanlauwe, B.; Akinnifesi, F.K.; Tossah, B.K.; Lyasse, O.; Sanginga, N.; Merckx, R. Root distribution of *Senna siamea* grown on a series of derived-savanna-zone soils in Togo, West Africa. *Agrofor. Syst.* **2002**, *54*, 1–12. doi:10.1023/a:1014203402176.
63. Zipper, C.E.; Burger, J.A.; Skousen, J.G.; Angel, P.N.; Barton, C.D.; Davis,

- V.; Franklin, J. Restoring Forests and Associated Ecosystem Services on Appalachian Coal Surface Mines. *Environ. Manag.* **2011**, *47*, 751–765. doi:10.1007/s00267-011-9670-z.
64. Buta, M.; Blaga, G.; Paulette, L.; Păcurar, I.; Roșca, S.; Borsai, O.; Grecu, F.; Sînziana, P.E.; Negrușier, C. Soil Reclamation of Abandoned Mine Lands by Revegetation in Northwestern Part of Transylvania: A 40-Year Retrospective Study. *Sustainability* **2019**, *11*, 3393. doi:10.3390/su11123393.
65. Larney, F.J.; Angers, D. A. The role of organic amendments in soil reclamation: A review. *Can. J. Soil Sci.* **2012** *92*, 19–38.
66. Mensah, A.K. Role of revegetation in restoring fertility of degraded mined soils in Ghana: A review. *Int. J. Biodivers. Conserv.* **2015**, *7*, 57–80. doi:10.5897/ijbc2014.0775.
67. Zhang, H.; Duan, H.; Song, M.; Guan, D. The dynamics of carbon accumulation in Eucalyptus and Acacia plantations in the Pearl River delta region. *Ann. For. Sci.* **2018**, *75*, 40. doi:10.1007/s13595-018-0717-7.
68. Clemmensen, K.E.; Bahr, A.; Ovaskainen, O.; Dahlberg, A.; Ekblad, A.; Wallander, H.; Stenlid, J.; Finlay, R.D.; Wardle, D.A.; Lindahl, B.D. Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. *Science* **2013**, *339*, 1615–1618. doi:10.1126/science.1231923.
69. Dong, J.; Kaufmann, R.K.; Myneni, R.; Tucker, C.J.; E Kauppi, P.; Liski, J.; Buermann, W.; Alexeyev, V.; Hughes, M.K. Remote sensing estimates of boreal and temperate forest woody biomass: carbon pools, sources, and sinks. *Remote Sens. Environ.* **2003**, *84*, 393–410. doi:10.1016/s0034-4257(02)00130-x.
70. Meli, P.; Holl, K.D.; Benayas, J.M.R.; Jones, H.P.; Jones, P.C.; Montoya, D.; Mateos, D.M. A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. *PLoS ONE* **2017**, *12*, e0171368. doi: 10.1371/journal.pone.0171368.
71. Srinivas, K.; Sundarapandian, S. Biomass and carbon stocks of trees in

- tropical dry forest of East Godavari region, Andhra Pradesh, India. *Geol. Ecol. Lands.* **2018**, 3, 114–122. doi:10.1080/24749508.2018.1522837.
72. Gandhi, D.S.; Sundarapandian, S. Large-scale carbon stock assessment of woody vegetation in tropical dry deciduous forest of Sathanur reserve forest, Eastern Ghats, India. *Environ. Monit. Assess* **2017**, 189, 604. doi:10.1007/s10661-017-5899-1.
73. Lung, M.; Espira, A. The influence of stand variables and human use on biomass and carbon stocks of a transitional African forest: Implications for forest carbon projects. *For. Ecol. Manag.* **2015**, 351, 36–46. doi: 10.1016/j.foreco.2015.04.032.
74. Padmakumar, B.; Sreekanth, N.; Shanthiprabha, V.; Paul, J.; Sreedharan, K.; Augustine, T.; Jayasooryan, K.; Rameshan, M.; Mohan, M.; Ramasamy, E.; Thomas, A. Tree biomass and carbon density estimation in the tropical dry forest of Southern Western Ghats, India. *iFor. —Biogeosci. For.* **2018**, 11, 534–541. doi:10.3832/ifer2190- 011.
75. Liu, F.; Gao, C.; Chen, M.; Li, K. Above- and below-ground biomass relationships of *Leucaena leucocephala* (Lam.) de Wit in different plant stands. *PLoS ONE* **2018**, 13, e0207059. doi: 10.1371/journal.pone.0207059.
76. Jiang, Y.; Zhang, Y.-J.; Wu, Y.; Hu, R.; Zhu, J.; Tao, J.; Zhang, T. Relationships between aboveground biomass and plant cover at two spatial scales and their determinants in northern Tibetan grasslands. *Ecol. Evol.* **2017**, 7, 7954–7964. doi:10.1002/ece3.3308.
77. Du, H.; Liu, L.; Su, L.; Zeng, F.; Wang, K.; Peng, W.; Zhang, H.; Song, T. Seasonal Changes and Vertical Distribution of Fine Root Biomass During Vegetation Restoration in a Karst Area, Southwest China. *Front. Plant Sci.* **2019**, 9. doi:10.3389/fpls.2018.02001.
78. Sun, T.; Hobbie, S.E.; Berg, B.; Zhang, H.; Wang, Q.; Wang, Z.; Hättenschwiler, S. Contrasting dynamics and trait controls in first-order root compared with leaf litter decomposition. *Proc. Natl. Acad. Sci. USA* **2018**,

- 115, 10392–10397. doi:10.1073/pnas.1716595115.
79. Manaye, A.; Negash, M.; Alebachew, M. Effect of degraded land rehabilitation on carbon stocks and biodiversity in semi-arid region of Northern Ethiopia. *For. Sci. Technol.* **2019**, *15*, 70–79. doi:10.1080/21580103.2019.1592787.
80. Chen, S.; Wang, W.; Xu, W.; Wang, Y.; Wan, H.; Chen, D.; Tang, Z.; Tang, X.; Zhou, G.; Xie, Z.; Chen, S., Wang, W., Xu, W., Wang, Y., Wan, H., Chen, D., Tang, Z., Tang, X., Zhou, G., Xie, Z., Zhou, D., Shangguan, Z., Huang, J., He, J., Wang, Y., Sheng, J., Tang, L., Li, X., Dong, M., Wu, Y., Wang, Q., Wang, Z., Wu, J., Chapin, F. and Bai, Y., 2018. Plant diversity enhances productivity and soil carbon storage. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 4027–4032. doi:10.1073/pnas.1700298114.
81. Meng, S.; Jia, Q.; Zhou, G.; Zhou, H.; Liu, Q.; Yu, J. Fine Root Biomass and Its Relationship with Aboveground Traits of *Larix gmelinii* Trees in Northeastern China. *Forest* **2018**, *9*, 35. doi:10.3390/f9010035.
82. Sollins, P. Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology* **1998**, *79*, 23–30.
83. Jeon, I.; Nam, K. Change in the site density and surface acidity of clay minerals by acid or alkali spills and its effect on pH buffering capacity. *Sci. Rep.* **2019**, *9*, 9878. doi:10.1038/s41598-019-46175-y.
84. Goulding, K.W.T. Soil acidification and the importance of liming agricultural soils with particular reference to the United Kingdom. *Soil Use Manag.* **2016**, *32*, 390–399. doi:10.1111/sum.12270.
85. Kumar, R.; Pandey, S.; Pandey, A. Kumar. Plant roots and carbon sequestration. *Curr. Sci.* **2006**, *91*, 85-890.
86. De Deyn, G.B.; Shiel, R.S.; Ostle, N.; McNamara, N.P.; Oakley, S.; Young, I.; Freeman, C.; Fenner, N.; Quirk, H.; Bardgett, R.D. Additional carbon sequestration benefits of grassland diversity restoration. *J. Appl. Ecol.* **2010**, *48*, 600–608. doi:10.1111/j.1365-2664.2010.01925. x.
87. Zhao, Y.; Krzic, M.; Bulmer, C.E.; Schmidt, M.G.; Simard, S.W. Relative

bulk density as a measure of compaction and its influence on tree height.

Can. J. For. Res. **2010**, *40*, 1724–1735. doi:10.1139/x10-115

88. Haile, W.; Boke, S. Response of Irish Potato (*Solanum tuberosum*) to the Application of Potassium at Acidic Soils of Chencha, Southern Ethiopia. *Int. J. Agric. Biol.* **2011**, *13*, 595–598.



© 2020 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).

Chapter IV: The Functional Structure of Tropical Plant Communities and Soil Properties Enhance Ecosystem Functioning and Multifunctionality in Different Ecosystems in Ghana

Published: 12th February 2022 in **Forests** 2022, 13, 297

<https://doi.org/10.3390/f13020297>

Frederick Gyasi Damphey^{1*}, Klaus Birkhofer¹, Imma Oliveras Menor^{2,3} and Enrique G. de la Riva¹

¹ Department of Ecology, Brandenburg University of Technology,
03046 Cottbus, Senftenberg, Germany
frederickGyasi.Damphey@b-tu.de (F.G.D.)
klaus.birkhofer@b-tu.de (K.B.)
enrique.garciadelariva@b-tu.de (E.G.d.I.R.)

² UMR AMAP: Botanique et Modélisation de l'Architecture des Plantes et des Végétations, Institute de Recherche pour de Développement (IRD), CNRS, INRAE CIRAD, Université Montpellier, 34090 Montpellier, France

³ Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 2JD, UK
imma.oliveras@ouce.ox.ac.uk (I.O.M.)

***Corresponding author**



Article

The Functional Structure of Tropical Plant Communities and Soil Properties Enhance Ecosystem Functioning and Multifunctionality in Different Ecosystems in Ghana

Frederick Gyasi Damp^{1,*}, Klaus Birkhofer¹, Imma Oliveras Menor^{2,3} and Enrique G. de la Riva¹

¹ Department of Ecology, Brandenburg University of Technology, 03046 Cottbus, Senftenberg, Germany; Klaus.birkhofer@b-tu.de (K.B.); Enrique.garciadelariva@b-tu.de (E.G.d.I.R.)

² UMR AMAP. Botanique et Modélisation de l'Architecture des Plantes et des Végétations, Institute de Recherche pour de Développement (IRD), CNRS, INRAE CIRAD, Université Montpellier, 34090 Montpellier, France; imma.oliveras@ouce.ox.ac.uk

³ Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 2JD, UK

* Correspondence: FrederickGyasi.Damp¹@b-tu.de

Received: 11 January 2022; Accepted: 7 February 2022; Published: 12 February 2022

Abstract

Plant functional traits are useful in tracking changes in the environment, and play an important role in determining ecosystem functioning. The relationship between plant functional traits and ecosystem functioning remains unclear, although there is growing evidence on this relationship. In this study, we tested whether the functional structure of vegetation has significant effects on the provision of ecosystem services. We analysed plant trait composition (specific leaf area, leaf carbon and nitrogen ratio, isotopic carbon fraction, stem dry matter content, seed mass and plant height), soil parameters (nutrients, pH, bulk density) and proxies of ecosystem services (carbon stock, decomposition rate, invertebrate activity) in twenty-four plots in three tropical ecosystems (active restored and natural forests and an agroforestry plantation) in Ghana. For each plot, we measured above-ground biomass, decomposition rates of leaves and invertebrate activity as proxies for the provision of ecosystem services to evaluate (i) whether there were differences in functional composition and soil properties and their magnitude between ecosystem types. We further aimed to (ii) determine whether the functional structure and/or soil parameters drove ecosystem functions and multifunctionality in the three ecosystem types. For functional composition, both the leaf economic spectrum and seed mass dimension clearly separated the ecosystem types. The natural forest was more dominated by acquisitive plants than the other two ecosystem types, while the non-natural forests (agroforest and restored forest) showed higher variation in the functional space. The natural forest had higher values of soil properties than the restored forest and the agroforestry plantation, with the differences between the restored and agroforestry plantation driven by bulk density. Levels of ecosystem service proxies and multifunctionality were positively related to the functional richness of forest plots and were mainly explained by the differences in site conditions. Our study demonstrated the effects of functional forest structure on ecosystem services in different forest ecosystems located in the semi-deciduous forest zone of Ghana.

Keywords: functional traits; functional diversity; multifunctionality; plants; post-mining restorations; resource use strategies; tropical forest; West Africa

1. Introduction

The ability of an ecosystem to cope with and adapt to global change has been an emerging ecological research topic in the last decade [1,2]. Relevant advances are necessary to support ecosystem research that will inform policy or design land management or ecological restoration strategies [3]. Ecosystem services involve the functioning and properties of an ecosystem, usually driven by species diversity and composition [4–6]. Thus, approaches aiming to address the impacts of global changes require an understanding of how changes in biodiversity affect ecosystem functioning [7]. For instance, the relationship between species richness and ecosystem functioning has been discussed in numerous ecosystems [8–10]. However, there is a general agreement that the functional structure of the communities (the functional trait composition and diversity *sensu* Mouillot et al. [11]) is a better reflection of ecosystem functioning than species richness [12,13].

Different strategies are required by plants in the acquisition and utilisation of resources within their environment. These strategies are defined by traits related to fitness, affecting growth, reproduction, survival and mortality [14]. Functional traits are therefore used as proxies to explain species performance and their assembly within communities as well as their impact on ecosystem functioning [13,15,16]. In addition, trait components relate to above-ground biomass production [17–22] and provide initiative links to ecological mechanisms, especially for separating the selection and complementarity effects [23]. Furthermore, functional trait approaches have been used to explore the effects of soil, and topographic properties on variations in tree above-ground carbon stocks [24], with the impact of species composition on ecosystem function also evaluated using the same approach [12]. Traits hence offer a lens to assess how community

composition and diversity define ecosystem functioning and service delivery [7].

Traits include the whole plant characteristics (e.g., leaves, stems, seeds) that reflect the strategies used by plants to acquire resources, reproduce and compete in an ecosystem [16,25,26]. These strategies used by plants in acquiring, processing and investing resources could vary between species characterising different ecosystems and could also affect the functioning of ecosystems [13,17,27]. These variations in traits (e.g., leaves or stems) could explain species strategies that influence their performance and ecosystem functioning [28,29]. For instance, traits related to plant structure and physiology, such as specific leaf area (SLA), stem dry matter content (SDMC), and leaf nutrient concentration, determine the quality and quantity of the litter produced, which could subsequently indirectly influence the carbon (C) storage and decomposition rate of leaves [30,31]. Another central issue is understanding the links between functional diversity and ecosystem functions [12,32]. The coexistence of functional strategies not only allows fuller resource exploitation by the plant community as a whole across time and space [31,33], but also seems to be a key determinant for other ecosystem services, such as soil organism diversity and biotic control by insects [3,34–36]. Functional trait approaches hence provide a window to evaluate the role of the functional structure of plant communities influencing ecosystem functions [12,30,31]. Most studies frequently quantified single or very few ecosystem services [7]. However, to address questions on the simultaneous provision of multiple services and the development of efficient management strategies, progress is needed to understand how functional structure and synergies within ecosystem functioning translate into interactions between ecosystem services [3,37,38].

Drivers of biodiversity change that influence ecosystem processes and functioning include land-use, climate change and deforestation [39,40]. In the tropics, deforestation is a known major threat to biodiversity that subsequently impacts societies and hinders the functioning of ecosystems and the services

they provide [41–43]. Approaches to reversing and minimising deforestation impacts have revolved around agroforestry (food and tree production) and restoration activities (passive or active [44]). Restoration hence assists in the re-colonisation of plant species with diverse strategies in resource release, and helps to offset the losses from deforestation by reducing carbon emissions, while at the same time restoring vital ecosystem goods and services essential for human well-being [44–47].

This study used the functional trait approach to understand ecological processes in different ecosystem types (restored forest, agroforestry system and natural forest). To address this, studies have concluded that the intrinsic properties of each environment, such as edaphic factors, need to be incorporated in addition to functional traits to link community plant functional parameters and ecosystem processes [48]. Furthermore, previous evidence suggests that soil parameters and ecosystem properties may influence functional trait composition, and thus, these factors may not be independent of each other [49]. Thus, gaining knowledge of the dynamics of ecosystem processes in land management in relation to the functional traits of plant communities and their soil properties will provide critical information on ecosystem services. Specifically, we assessed: (i) whether there were differences in functional composition and soil properties and the magnitude of differences between the ecosystem types; and (ii) whether the functional structure and/or soil parameters drove ecosystem functions and multifunctionality in the three ecosystem types. To achieve the above aims, we analysed plant trait composition (SLA, C/N, $\delta^{13}\text{C}$, SDMC, S_{mass} and Phg), soil parameters (nutrients, pH, BD), and other ecosystem functions related to services (based on proxies) across an actively restored forest, agroforestry plantation and a natural forest in the semi-deciduous forest zone of Ghana. We considered the methodological framework proposed by previous studies [3,12,31] for the design of experimental tests of the relative roles of community-weighted means (CWM) and functional diversity in ecosystem processes based on

seven plant functional traits related to plant resource use and growth strategies. In addition, we relied on the carbon stock, decomposition rate of leaves, predators, and decomposing organism numbers as proxies to estimate the services derived from each ecosystem type.

2. Materials and Methods

2.1. Study Site Description

We analysed plant trait composition, soil parameters and ecosystem services across three ecosystem types (actively “restored forest”, RF; “agroforestry plantation”, AF; and “natural forest”, NF) in a semi-deciduous forest zone (SDFZ), all located in the Ahafo and Bono regions of Ghana (Figure 1). The zone has a mean daily temperature of 20 °C, mean annual precipitation ranging between 900 and 1500 mm (rainfall peak between July and August [45]) and a soil classification according to the United States Department of Agriculture (USDA) Soil Taxonomy and the Food and Agriculture Organisation (FAO) World Reference Base as Ultisols (Acrisols and Nitisols) in the uplands and Fluvents (Fluvisols) and Inceptisols (Cambisols) in the lowlands [45].

The RF located in Terchire (7°14'4.78" N, 2°10'49.88" W) is a post mine area that has been actively restored with both indigenous and exotic tree species (e.g., *Morinda lucida* Benth, *Terminalia suberba* Engl. & Diels, *Albizia zygia* (DC.) J. F. Machr., *Cedrela odorata* L., *Mangifera indica* L.) after soil improvement to provide essential ecosystem goods and services to society. On the other hand, AF (7°6'20.76" N, 2°15'22.64" W) is a forest reserve experiencing massive degradation. Because of its degraded nature, it has been subjected to agroforestry programs (food crops interplant with trees) to supply both food and energy needs as well as environmental benefits to fringe communities. In contrast, NF (7°9'13.72" N, 2°31'4.96" W) is a protected forest reserve under strict restrictions against anthropogenic activities [44].

2.2. Data Collection

We analysed plant trait composition, soil properties and ecosystem services across the three ecosystem types (actively “restored forest”, RF; “agroforestry system”, AF; and “natural forest”, NF). To this end, we demarcated eight plots of sizes 20 × 20 m in each of the three ecosystem types to sample ecosystem services using proxies, plant traits and soil attributes. To quantify the species abundance and composition of each woody species in the rainy season, we counted and identified all trees with a diameter ≥ 10 cm at breast height (dbh) to species level with a local botanist’s assistance and a field manual [50]. We chose a minimum dbh threshold ≥ 10 cm as this threshold encompasses the main diversity of tropical forest trees [51]. Then, we calculated each identified tree’s above-ground biomass using an improved allometric equation for the pantropical region [$\ln(\text{AGB}) = \alpha + \beta \ln(\rho \times D^2 \times H) + \varepsilon$; [52]] based on tree dbh, estimated height, and specific wood density values of trees obtained from the global wood density database [53].

2.3. Ecosystem Functions and Multifunctionality

Except We relied on the carbon stock, decomposition rate, pest regulation activities of predators, and decomposing organism numbers as proxies to estimate our study forest plots’ ecosystem services. In estimating carbon dioxide storage in tree tissues, the carbon stock was assumed to be 50% of the calculated above-ground biomass of each tree for each forest plot expressed per hectare [54]. Decomposition (the rate by which nutrients from plant tissues such as leaves are released back into the ecosystem through the activities of detritivores arthropods [55]) was estimated with a standardised method involving the use of tea bags as a proxy [56]. Regulating (control of pests) and supporting (organic matter decomposition) ecosystem services were also estimated using predators and decomposing organism numbers as proxies [44].

In sampling these organisms, we relied on five pitfall traps in each plot for each ecosystem type. Arthropod sampling was performed for ten weeks (June to August 2019) and was emptied weekly. Trapped samples were taxonomically grouped according to the available literature (order, suborder or family) and subsequently classified into major functional groups (decomposers as supporting services and predators as regulating service providers).

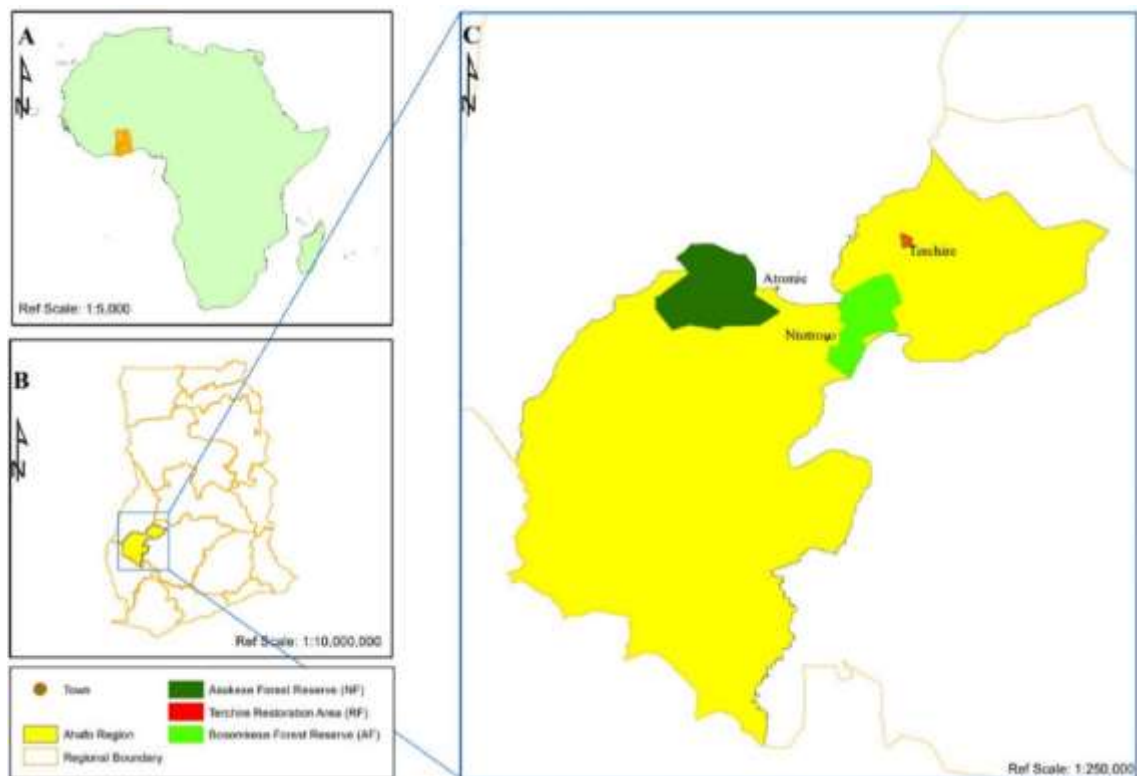


Figure 1. Map of the study region with the various ecosystem types. (A) Africa, (B) Ghana and (C) Ahafo region

2.4. Functional Composition and Diversity

We ranked the species by their relative abundances for trait measurements and selected those species representing at least 90% of the total plant woody abundance measured in each plot. This resulted in a total of 38 different sampled species, many of which appeared in more than one sampling forest type (Appendix A, Table A1), from which 7 plant functional traits (Table 1) related to

plant resource use (water, nutrient and light), reproductive effort and growth strategies were measured.

Trait attributes were collected in July 2020 (the peak biomass production period when rainfall was at its peak in the study region), except for seed mass compiled from seed databases available from the TRY Plant Trait Database [57] and the Royal Botanic Gardens, <http://data.kew.org/sid/> (accessed on 28 August 2021). We selected 4 individuals of a species from each ecosystem type, constituting 152 individual trees per ecosystem type and 456 trees for the entire study. The chosen trees were canopy trees with leaves exposed to the sun and no visible damage. Therefore, we sampled 4 to 8 leaves from the 4 individual trees of each species. Fresh leaf and stem samples were first weighed and dried to a constant temperature of approximately 70 °C for 72 h. Before drying the leaf samples, their area was scanned (with Canon CanoScan LiDE 300 Flatbed Scanner; Canon Inc., Tokyo, Japan), images were uploaded onto ImageJ software [58], and leaf area was calculated following Glozer [59]. All trait measurements were carried out according to the criteria and methodology defined by Pérez-Harguindeguy et al. [60].

Table 1. Plant functional traits sampled and their respective functional roles in the ecosystem.

Organ	Trait	Abb	Unit	Functional Role	References
Leaf	Specific leaf area	SLA	m ² kg ⁻¹	Reflects whole-plant growth and photosynthetic efficiency of a species	[61,62]
	Leaf carbon and nitrogen ratio	C/N		It is an indicator of nitrogen-use efficiency reflecting the metabolic status of C and N in leaves	[63,64]
	Isotopic carbon fraction	δ ¹³ C	‰	Reflects gas exchange and water-use efficiency	[65]
Stem	Stem dry matter content	SDMC	mg g ⁻¹	Relates above-ground storage of carbon and stimulates plants' resistance to physical hazards	[33,66]
Seed	Seed mass	Smass	mg	Moderates a trade-off between plants' rate of seed production per unit mass invested in reproduction and the mass of each offspring	[67]
Whole plant	Plant height	Phg	m	Reflects a species ability to utilize light and above the ground competition	[68,69]

SLA was calculated as leaf area divided by the leaf dry mass, while the SDMC was calculated by dividing the oven-dry weight of the stem by the fresh weight. Leaf chemical traits, including carbon, nitrogen and isotopic carbon ($\delta^{13}\text{C}$), were analysed at the Centre for Stable Isotope Research and Analysis (George August Universität, Göttingen, Germany). Seed mass for each species was obtained from the TRY Plant Trait Database [57] and the Royal Botanic Gardens (<https://data.kew.org/sid/>, accessed on 28 August 2021), while plant height (the vertical distance from the topmost living or dead part of the tree to the upslope side of the trunk base; [70]) for each tree was measured using Nikon Forestry pro II Laser Rangefinder/Hypsometer.

The functional composition of each community was obtained following Garnier

et al. [71]. First, the traits were weighted by the relative abundance of their constitutive species to calculate the community weighted mean (CWM) in each plot. Then, we estimated the functional diversity per community based on functional richness (Frich) and Rao's quadratic entropy (RaoQ [72–76]). Frich represents the amount of the functional space, where each trait is a dimension occupied by all the species present and characterises the change in functional space caused by the difference in the community structure [74,75]. RaoQ integrates the relative abundances of species with a measure of the pairwise functional differences between species [76,77].

2.5. Soil Properties Measurement

We took replicated soil samples (five samples combined into a composite sample) from each plot and ecosystem to analyse physical and chemical properties in the laboratory. The soil properties analysed included nutrient concentrations (nitrogen, phosphorus, magnesium, sodium, potassium and soil organic concentration—SOC), pH, and bulk density (BD). For the methodological details involved in sampling and analysis, see Damptey et al. [45].

2.6. Data Analysis

First, to identify major axes of attribute covariation and reduce the dataset to the same functional dimensions per component (soil parameters—SP; functional composition—FC; ecosystem services—ES), which is specially recommended for hypervolume analysis [78], we performed principal component analysis (PCA). We performed one PCA for each component with the mean value per plot of their attributes for ES (carbon stock, decomposition rate, pest control and decomposers) and SP (N, P, Mg, Na and K concentration, pH, BD and SOC) and the CWM for FC (SLA, SDMC, C/N, $\delta^{13}\text{C}$, Phg and Smass). We used the first three principal components for posterior analyses. To explore the distinctiveness between ecosystem types for soil properties and functional composition, we calculated the mean effect size (Hedges'd) and bias-corrected

95% bootstrap confidence intervals (effsize package [79]). The mean effect size was considered significantly different from zero when its confidence interval did not bracket zero.

Then, to assess the degree of similarity among the three ecosystem types for each study component independently (SP, FC and ES), we used the first three PCA axes to calculate each component's hypervolume (SP, FC and ES) using a multidimensional kernel density estimation procedure. This approach quantified the magnitude of the occupied functional space by the n-dimensional space method [80]. First, we calculated the total amount of the multidimensional space occupied by each component independently. The estimation of the n-dimensional hypervolume calculated this multidimensional space for each component and ecosystem type. Then, we calculated the overlap between the hyper- volumes among ecosystem types for each component with the correlation analysis of the "hypervolume" package, which compared the similarity between different hypervolumes using the Sørensen index [81].

To determine which attributes of the functional structure (functional trait composition and diversity) and soil parameters were best associated with each ecosystem service and multifunctionality, we conducted maximum likelihood techniques with a linear function using the likelihood package. We only fitted three-factor models to avoid overestimating the models with spurious parameters with very poor weights [82]. The factors were added either additively or multiplicatively. Due to the influence of ecosystem type on the functional composition and soil properties (as we observed in the effect size results), we also included the factor "ecosystem type" as a block factor. Then, models were ranked by their Akaike information criterion (AICc), and corrected for small sample size [83]. Models were considered to be equally supported if the difference in AIC was less than two units.

All statistical analyses were performed, producing all figures in the R 3.6.1 statistical platform [84].

3. Results

The first three components of the PCA accumulated 70.01%, 71.65% and 93.06% for SP, FC and ES, respectively (Table 2). The first principal component of the soil properties (explaining 32.30% of the variance) represented a gradient of soil nutrient availability (concentration of soil nitrogen, potassium, sodium and organic matter). In comparison, the second PCA axis (22.87%) was mainly associated with differences in the pH and concentration of soil phosphorus, and the third component (14.84%) was related to bulk density. With regard to the functional composition, the first principal component (34.27%) reflected coordination between SLA (specific leaf area) and $\delta^{13}\text{C}$ (isotopic carbon fraction), which is representative of the leaf economics spectrum, and seed mass. The second principal component (20.70%) reflected a covariation in tissue resistance, as reflected by the gradient in SDMC (stem dry matter content) and C/N, while the third component (16.68%) was defined by plant height. The first component of the ecosystem services (39.69%) reflected invertebrate activity in both pest control and decomposition (higher abundance of predators and decomposers), while the second (30.34%) and third (23.03%) were linked to carbon stock and decomposition rate, respectively. Most functional traits values were higher in the natural forest than the other ecosystem types (Appendix A, Table A2).

Table 2. Variance partitioning of trait attributes for the three ecosystem types.

Soil properties	Source of Variance		
	PC1	PC2	PC3
pH	4.0	61.0	7.0
N	50.0	14.0	23.0
P	15.0	62.0	15.0
K	55.0	2.0	4.0
Na	47.0	14.0	8.0
Mg	14.0	17.0	38.0
SOC	42.0	21.0	49.0
BD	4.0	37.0	72.0
% variance	32.3	22.9	14.8
Functional composition			
SLA	53.0	24.0	12.0
SDMC	2.0	64.0	44.0
Seed mass	46.0	33.0	33.0
C:N	37.0	56.0	23.0
$\delta^{13}\text{C}$	52.0	30.0	36.0
Plant height	29.0	13.0	71.0
% variance	34.3	20.7	16.7
Ecosystem service proxies			
Carbon stock	10.0	78.0	46.0
Predator no.	68.0	27.0	26.0
Decomposer no.	72.0	13.0	20.0
Decomposition rate	2.0	55.0	83.0
% variance	39.7	30.3	23.0

3.1. The relationship of Ecosystem Types with Soil Parameters and Functional Composition

Overall, natural forest showed greater soil properties (higher nutrient concentration and lower bulk density) than non-natural forests (restored and agroforestry) (Figure 2), with the differences among restored forest and agroforestry plantation determined by bulk density (Figure 2). The functional space was greatest for the restored forest (257.60 sd³) (Figure 3A), representing higher soil variability than the natural forest (65.67 sd³) and agroforestry plantation (77.49 sd³). The restored forest and agroforestry plantation showed a higher functional space overlap (35%) in terms of soil properties. However, the percentage of functional space overlap in the natural forest was higher than that in the restored forest (29%) and the agroforestry plantation (26%; Figure 3A).

In terms of functional structure, the main differences among the types of ecosystems were determined by the leaf economic spectrum (LES) and seed mass dimension, showing higher values in the natural forest than in the restored forest and agroforestry plantation (Figure 2), which suggests that the functional composition of the natural forest was dominated by acquisitive plants with higher seed mass, in contrast with the non-natural forests. With regard to the functional composition (Figure 3B), the natural forest showed the lowest functional space (21.45 sd³), while the non-natural forest showed higher variation (agroforest 140.19 sd³ and restored 109.40 sd³). However, for the functional space overlaps, the pattern was the same for soil properties, showing that the restored forest and agroforestry plantation had the highest overlap (45%), while the natural forest was more similar to the restored forest (24%) than the agroforestry plantation (19%; Figure 3B).

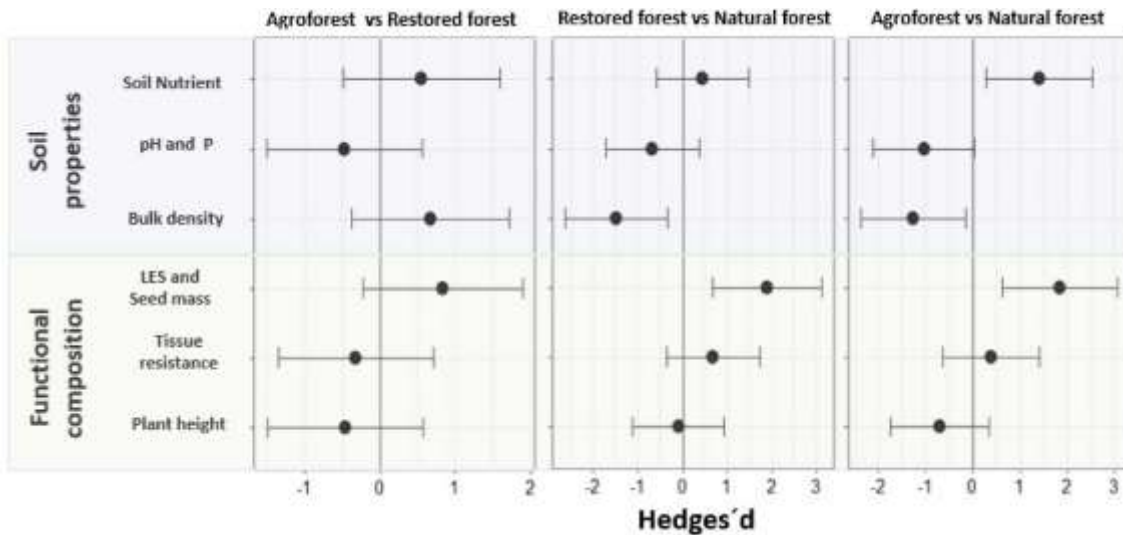


Figure 2. Mean effect size (Hedges'd) and bias-corrected 95% bootstrap confidence intervals for differences between the ecosystem types for each PC dimension of the functional composition and soil parameters (see Table 2).

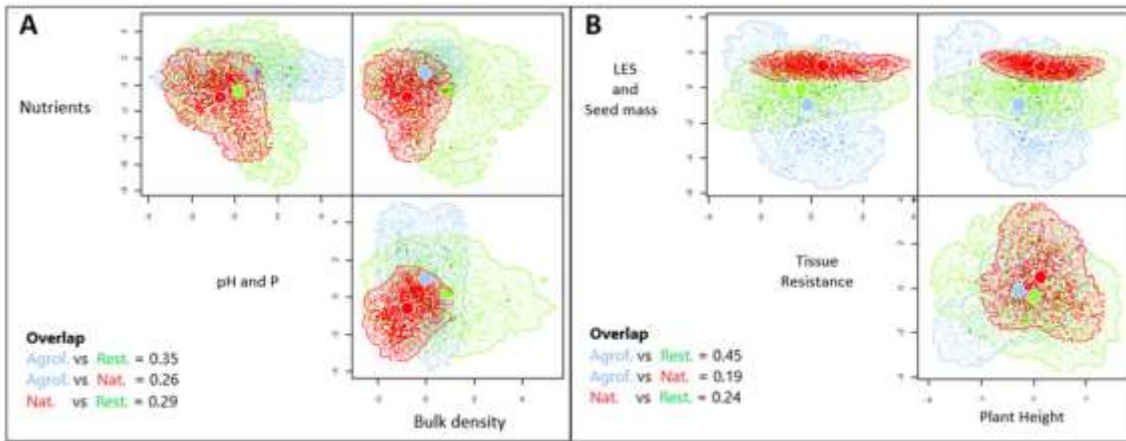


Figure 3. Estimated three-dimensional hypervolumes for the three ecosystem types (see Table 2). Each plant dimension was based on the first PCA axis of the different attributes belonging to soil properties (A) and functional trait (B) dimensions. Overlap among each type of ecosystem based on the Sørensen similarity index is shown.

3.2. The Influence of Functional Structure and Soil Properties on Ecosystem Services and Multifunctionality across Ecosystems

The results from the n-dimensional hypervolume revealed similar variability among the three ecosystem types (63.55 sd³ for natural, 69.06 sd³ for restored and 58.70 sd³ for agroforest). In contrast with the previous dimensions (SP and FC), the restored and natural forests were more similar (45%) than the restored forest and agroforestry plantation (31%) and agroforestry plantation and natural forest (21%; Appendix A, Figure A1).

Our results showed that the ecosystem services and multifunctionality were explained mainly by the differences in site conditions of each ecosystem (except for decomposition rate), with FRic providing supplementary explanations independent of the selected ecosystem (additive interactions in all cases; Table 3). Hence, our model confirmed invertebrate activity, carbon stock and multifunctionality to be influenced by the differences in ecosystems and positively related to FRic ($R^2 = 0.52$, $R^2 = 0.58$, $R^2 = 0.47$, respectively). Furthermore, pairwise comparison (Tukey post-hoc test) among ecosystem types showed the highest carbon stock (Appendix A, Figure A2) and multifunctionality (Figure 4) in the natural forest, rather than in the non-natural forests, while both the natural and restored forests showed higher invertebrate activity than agroforestry plantation (Appendix A, Figure A2). In contrast, the decomposition rate was mostly determined by a negative relationship with the soil bulk density dimension ($R^2 = 0.24$; Table 3).

Table 3. Summary of the best-fitted models analysing ecosystem services in response to functional structure (composition and diversity) and soil factors. AICc = Akaike information criterion for small samples; $\Delta AICc$ = difference between the AICc of a null model and the best model ($\Delta AIC < 2$ in all cases).

Ecos. Service	Factors	Relation	R ²	AICc	$\Delta AICc$
Invertebrate activity	Null Model			80.36	
	Site+Frich	+	0.52	71.42	0.00
Carbon stock	Null Model			72.28	
	Site+Frich	+	0.58	60.94	0.00
Decomposition Rate	Null Model			67.97	
	Soil BD	-	0.24	64.38	0.00
Multifunctionality	Null Model			10.57	
	Site+Frich	+	0.47	3.82	0.00

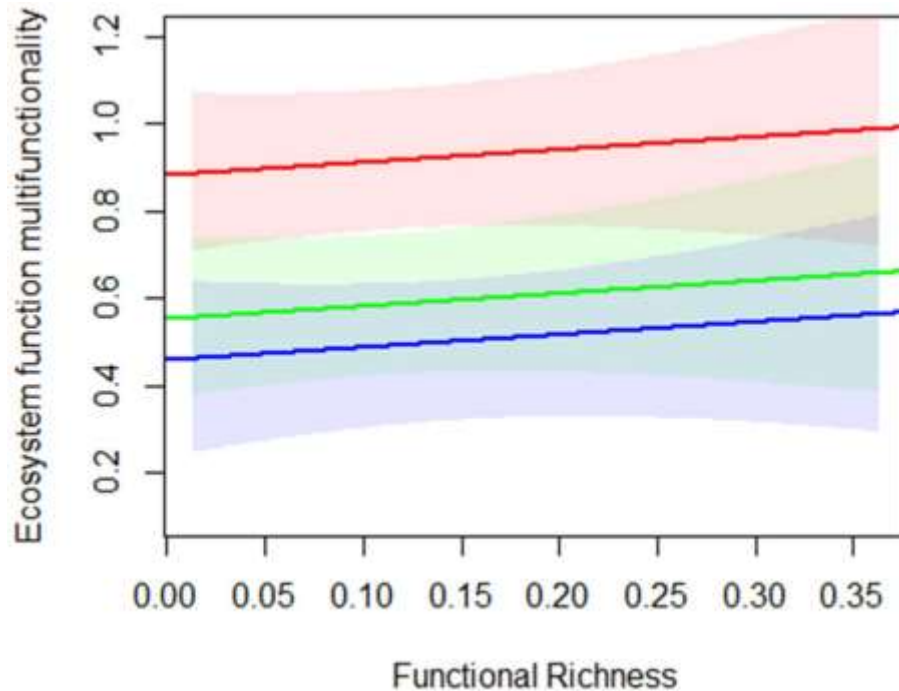


Figure 4. Relationship between ecosystem multifunctionality and functional richness per site (natural forest in red, restored forest in green and agroforestry plantation in blue). The shaded area shows 95% confidence intervals.

4. Discussion

In general, we observed differences in the functional space of soil properties, trait composition and ecosystem service proxies between the three ecosystem types. This study highlights the positive role of functional structure (mainly functional richness) of plant communities in driving ecosystem functioning and multifunctionality. The differences in the functional space of ecosystem services and trait compositions between ecosystem types resulted from different management decisions. Interestingly, the restored forest took an intermediate position between the natural forest and the agroforestry plantation for the studied dimensions. That is, the restored forest showed higher similarity for all the study dimensions with the natural forest than the agroforestry plantation, indicating a successful trajectory of the post-mining area under restoration over time.

4.1. Ecosystem Type Relationship with Soil Parameters and Functional Composition

In terms of soil properties, we observed the natural forest to have overall better soil attributes than the other ecosystem types, which was quite expected because of the natural forest age, level of protection, and plant species pool. Nevertheless, lower nutrient concentrations but higher pH and phosphorus levels were observed for the agroforestry plantation. This phosphorus concentration might have been caused by the excessive use of fertilisers (both organic and inorganic) for crop farming in the agroforestry plantation. In an agroforestry plantation, farmers inter-planting food crops with trees rely on fertilisers when natural remedies are insufficient to yield optimal results within the shortest possible time. This might have subsequently led to an increase in soil pH because of the alkaline nature of some applied fertilisers [85]. In contrast, soil fertility and pH in the restored forest did not differ significantly from those in the natural forest. Nevertheless, this did not imply a high similarity in the soil properties of either type of ecosystem, which is explained by the highest bulk

density value in the restored forest. The high bulk density in the restored forest is due to the historical use of heavy machinery during the mining era. Although the restored forest seems to be on a recovery trajectory in soil development [45], its higher bulk density is due to some compaction issues that could improve with time.

This study also detected a consistent variation in the functional trait composition among the natural and non-natural forests (restored forest and agroforestry plantation). That is, the hypervolumes of the natural forest showed low overlap in terms of functional composition with regard to the others. This is not surprising because, in a previous study, we observed strong differences in terms of plant composition among these three ecosystems [45]. The strong role of species turnover as the main driver of functional trait variation is in accordance with previous studies at the local scale in tropical (e.g., Oliveras et al. [86]) and temperate forests (e.g., de la Riva et al. [87]). Indeed, Oliveras et al. [86] reported a high species replacement along an elevational gradient in a tropical forest from Ghana, reflecting the strengths of local filtering in each type of ecosystem. However, the non-natural forests showed higher functional overlap among them in terms of species composition (see also Dampney et al. [45]). One of the main reasons could be the use of exotic tree species with similar traits, such as *Cedrela odorata* L., which increases the functional similarity of both non-natural forests compared with the natural forest. We found that the differences in the functional composition of the natural forest with regard to the non-natural forests were mainly determined by the dimension related to leaf economics spectrum theory (*sensu* Wright et al. [88]) and seed mass. Therefore, communities from the natural forest were dominated by fast-growing, acquisitive species with high resource uptake and low water and nutrient use efficiency (higher values of SLA and lower $\delta^{13}\text{C}$; [88,89]), and higher seed mass. This general pattern is consistent with previous studies where neotropical forests show higher values of SLA than less productive environments [90–92] because, in these productive habitats,

competition for light may promote the selection of resource-acquisitive species, where it is better to grow faster and compete for light [89,92]. Indeed, as the climatic variables (primarily temperature and precipitation) set broadly similar conditions among the three ecosystems, our observations suggest that the intrinsic properties of each environment, such as edaphic factors, determine the functional composition of the communities. For instance, the highest soil fertility enhances the acquisitive strategies of the natural forest, while the lower water (high BD) and nutrient availability promoted by land-use management over soil productivity, seem to favour species with long-term investment and nutrient retention in the non-natural forests. In addition, the faster resource acquisition strategy was also positively related to higher values of seed mass.

Similarly, Cornelissen [93] reported a positive relationship between leaf area and seed size in woody species. Overall, higher seed mass may enhance seedling success [94,95] at the expense of producing fewer seeds per unit of reproductive effort and reducing dispersal capability [96,97]. In a previous study, we also observed a higher biomass of food and fodder trees in the natural forest [44]. Since the size of the seeds in tropical trees is related to fruit size [98], this is probably a pattern resulting from historical selection by the local population that has favoured tree species with specific traits. Overall, our results provide novel insight into the effects of anthropogenic activity as the main driver of plant community assembly in tropical forests, pointing out that there is a strong pressure of certain functional strategies in non-natural management ecosystems.

4.2 Functional Structure and Soil Properties Influence Ecosystem Services and Multifunctionality across Ecosystems

We observed that invertebrate activity, carbon stock and multifunctionality were mainly driven by the specific properties of each ecosystem type, probably determined by the respective management focus (protection, convalescence or agroforestry). For instance, the natural forest had the highest

carbon stock, which is not surprising because mature tropical forests are frequently dominated by old trees with a high diameter [99,100]. We have previously identified higher above-ground biomass, root organic carbon content, and tree species richness in natural forest [44,45].

In addition, the observed association of invertebrates (predators and decomposers) could be a response of these groups to diverse vegetation and complexity of the stand structure, which probably results in the availability of various food resources and habitat niches [101,102]. However, the restored forest is mostly dominated by trees in younger stands with smaller diameters and above-ground biomass compared with the agroforestry plantation. Hence, the high number of invertebrates in the restored forest compared with the agroforestry plantation may result from different factors. The complex topsoil and soil surface structure in the restored forest [45] may enhance invertebrate activity. This complex topsoil serves as a habitat for numerous invertebrates providing shelter, protection, and food resources, as well as serving as breeding grounds [103]. On the other hand, the lower activity of invertebrates in the agroforestry plantation could be related to agricultural management practices in the area. For instance, the application of pesticides reduces many non-target invertebrate numbers [104]. Independent of the major driver, land-use intensification seems to result in a shift towards lower invertebrate activity in tropical tree-dominated ecosystems, supporting previous studies in the tropics [105], and globally [106,107].

The natural and restored forests shared the highest functional space for ecosystem services driven by carbon storage, regulating invertebrate activities (decomposers and pest control) and decomposition rates. A higher functional space overlap between the natural and restored forest ecosystem services could be related to both ecosystems sharing an almost similar volume of above-ground biomass, organic root carbon, and soil properties (see Damptey et al. [45]) emanating from the previous restoration interventions. This indicates successful ongoing ecological development of the

restored forest, which improves with better management options. Accordingly, available soil nutrients should help plants grow faster and increase biomass productivity [108,109]. Fertile soils in the natural and restored forests may have translated into higher tree species diversity and their functional attributes, thereby enhancing their carbon storage potentials (productivity [110–112]).

We also observed that functional richness and/or soil properties drive ecosystem functions and multifunctionality across ecosystem types [23,113,114]. The ability of each forest (ecosystem) to simultaneously perform multiple ecosystem functions (multifunctionality [115]), such as carbon storage, increasing decomposer abundance and pest control, is influenced positively by the functional richness of the particular ecosystem in question. Usually, diverse trees with multiple traits lead to efficient resource utilisation and subsequent improvement in ecosystem functioning, such as productivity [116,117], which may explain the positive relationship between functional richness and carbon stock. The role of functional diversity in carbon storage has been discussed extensively. For instance, a study by Mensah et al. [118] revealed a positive relationship between functional diversity (richness and evenness) and carbon storage. Similarly, Shen et al. [116] discussed the role of functional diversity in influencing carbon storage, which reflects the relative importance of complementarity effects [119]. Furthermore, invertebrate numbers (a proxy for pollinators, decomposers and pest regulators) also correlated positively with functional richness, in agreement with several studies [120,121]. This relationship resulted from the fact that diverse tree richness offered various ecological niches that supported the activities of most invertebrates, providing several ecosystem functions [122,123]. For instance, higher functional richness may provide suitable foraging and nesting resources, favour food web interactions, and support the survival and activities of invertebrates [124], thereby influencing ecosystem multifunctionality [125].

In addition, our results show negative feedback between decomposition rates and soil bulk density. The decomposition rate is strongly

influenced by soil bulk density [126] because soil compaction strongly promotes water limitations [127,128], reduces oxygen and limits nutrient transportation through soil constraining indigenous flora, plant root systems and soil organic matter [129]. Therefore, reduced aeration, characterizing soils with higher bulk density, has been postulated as a driver limiting the activities of soil- decomposing microbes [130]. In fact, in a previous study [45], we observed that bulk density also accounts for the variation in root organic carbon in these areas. Thus, variation in microbiota, soil invertebrates and root morphology due to varying soil BD may affect decomposition rates [129,131,132].

5. Conclusions

Our study highlights that tropical tree-dominated ecosystems with higher functional diversity are superior in providing multiple ESs, compared to less functionally diverse forests [133–135]. Higher functional richness of tree communities holds the potential to enhance ecosystem multifunctionality, independent of the ecosystem type. From the results of this study, it is evident that it is crucial to preserve natural and restored forests as key reservoirs of ecosystem services, especially in tropical countries such as Ghana, where deforestation continues to threaten the livelihoods of local human communities and biodiversity *per se*. It is also essential to develop appropriate restoration protocols and management strategies that could favour functional diversity and soil properties in tropical forests to enhance the provision of ecosystem services.

Author Contributions: All authors contributed to the study conception and design. F.G.D. wrote the first draft of the manuscript and all authors commented on previous versions. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Institutional Consent Statement: Not applicable.

Data Availability Statement: The data that support the findings of this study are openly available in figshare. Available online: <https://figshare.com/s/30cd2df0f3db5b96e135>.

Acknowledgments: We are grateful to the Newmont Gold Ghana Limited, Forest Service Division of Ghana and the Terchire community for making the study sites available. We would like to thank the reviewers and the editor for their comments on a previous version. We appreciate the contributions of Daniel Kwame Debrah, Prince Pascal Agro, and Clement Wulnye during the fieldwork. We are grateful to the Centre for Stable Isotope Research and Analysis (George August Universität, Göttingen, Germany) for helping with the nitrogen and isotopic carbon analysis. Scholarship support from the Catholic Academic Exchange Service (KAAD) to FGD is greatly appreciated.

Conflicts of Interest: On behalf of all authors, the corresponding author states no conflict of interest.

Appendix A

Table A1. Tree species considered for trait measurement. Family names of species adopted from The Plant List [136].

Species	Family
<i>Antrocaryon micraster</i> A. Chev. & Guillaumin	Anacardiaceae
<i>Alstonia boonei</i> De Wild.	Apocynaceae
<i>Funtumia elastica</i> (Preuss) Stapf	Apocynaceae
<i>Holarrhena floribunda</i> (G. Don) T. Durand & Schinz	Apocynaceae
<i>Rauvolfia vomitoria</i> Afzel.	Apocynaceae
<i>Spathodea campanulata</i> P. Beauv.	Bignoniaceae
<i>Distemonanthus benthamianus</i> Baill.	Leguminosae
<i>Terminalia ivorensis</i> A. Chev.	Combretaceae
<i>Terminalia suberba</i> Engl. & Diels	Combretaceae
<i>Antidesma laciniatum</i> Müll. Arg.	Phyllanthaceae
<i>Macaranga barteri</i> Müll. Arg	Euphorbiaceae
<i>Albizia zygia</i> (DC.) J. F. Macbr.	Leguminosae
<i>Anthocleista nobilis</i> G. Don	Gentianaceae
<i>Amphimas pterocarpoides</i> Harms	Leguminosae
<i>Bombax buonopozense</i> P. Beauv.	Malvaceae
<i>Ceiba pentandra</i> (L.) Gaertn.	Malvaceae
<i>Cola gigantea</i> A. Chev.	Malvaceae
<i>Mansonia altissima</i> (A Chev.) A Chev.	Malvaceae
<i>Pterygota macrocarpa</i> K. Schum.	Malvaceae
<i>Azadirachta indica</i> A. Juss.	Meliaceae
<i>Entandrophragma angolense</i> (Welw.) C. DC.	Meliaceae
<i>Entandrophragma utile</i> (Dawe & Sprague) Sprague	Meliaceae
<i>Khaya anthotheca</i> (Welw.) C. DC.	Meliaceae
<i>Piptadeniastrum africanum</i> (Hook.f.) Brenan	Leguminosae
<i>Antiaris toxicaria</i> (Lesch.)	Moraceae
<i>Ficus exasperata</i> Vahl	Moraceae
<i>Milicia excelsa</i> (Welw.) C. C. Berg	Moraceae
<i>Morus mesozygia</i> Stapf	Moraceae
<i>Pycnanthus angolensis</i> (Welw.) Warb.	Myristicaceae
<i>Margaritaria discoidea</i> (Baill.) G. L. Webster	Phyllanthaceae
<i>Morinda lucida</i> Benth.	Rubiaceae
<i>Blighia sapida</i> K.D. Koenig	Sapindaceae
<i>Chrysophyllum albidum</i> G. Don	Sapotaceae
<i>Sterculia rhinopetala</i> K. Schum.	Malvaceae
<i>Celtis adolfi-friderici</i> Engl.	Cannabaceae
<i>Celtis mildbraedii</i> Engl.	Cannabaceae

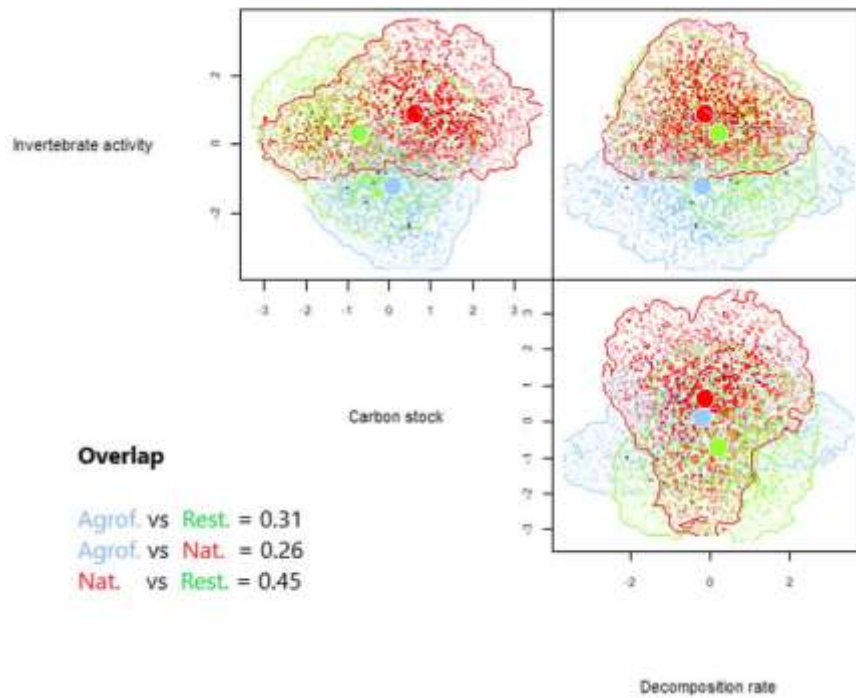


Figure A1. Estimated three-dimensional hypervolumes for the three study sites (see Table 2). Each plant dimension was based on the first PCA axis of the different attributes belonging to ecosystem services dimensions. Overlap among each type of forest based on Sørensen similarity index is shown.

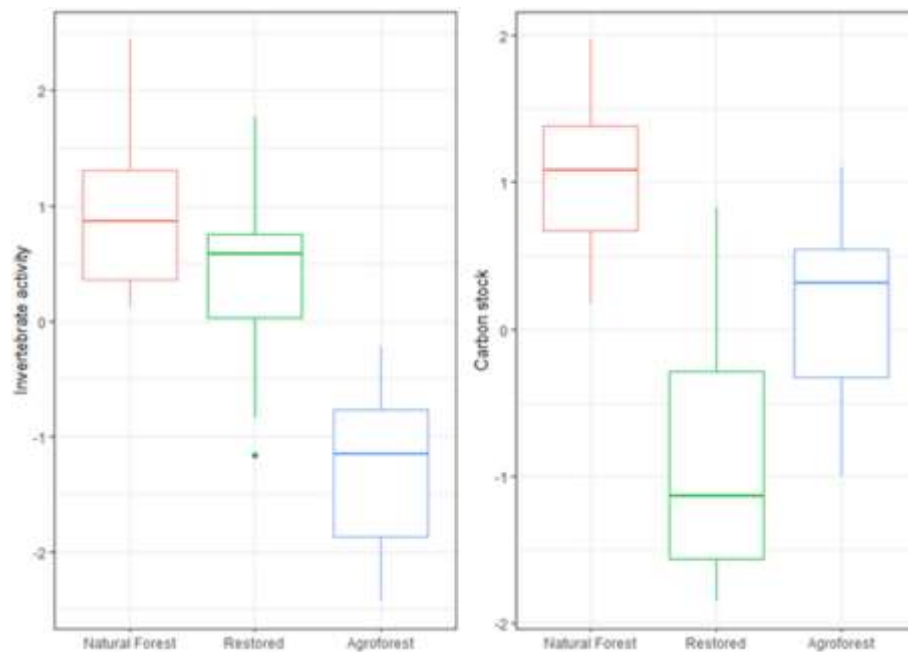


Figure A2. Boxplot between ecosystem types and ecosystem services dimensions (PC1—invertebrate activity; PC2—carbon stock dimensions) (see Table 2). The line inside the box represents the median value, the box limits are the 25th and 75th percentiles, error bars show 10th and 90th percentiles.

Table A2. Functional trait values (averages) for ecosystem types

Plant abundance and measured functional traits	Natural forest	Restored forest	Agroforestry plantation
Plant abundance (n/ha)	157	119	153
Specific leaf area (m/kg ²)	80.646	66.326	47.018
Leaf carbon and nitrogen ratio	13.292	12.192	12.480
Isotopic carbon fraction (‰)	31.117	31.174	30.523
Stem dry matter content (mg/g ¹)	0.423	0.411	0.418
Seed mass (mg)	0.907	0.569	0.666
Plant height (m)	14.532	14.655	16.120

References

1. Malhi, Y.; Franklin, J.; Seddon, N.; Solan, M.; Turner, M.G.; Field, C.B.; Knowlton, N. Climate change and ecosystems: Threats, opportunities and solutions. *Philos. Trans. R. Soc. B Biol. Sci.* **2020**, *375*, 1794. [[CrossRef](#)] [[PubMed](#)]
2. Van der Geest, K.; de Sherbinin, A.; Kienberger, S.; Zommers, Z.; Sitati, A.; Roberts, E.; James, R. The impacts of climate change on ecosystem services and resulting losses and damages to people and society. In *Loss and Damage from Climate Change*; Mechler, R., Bouwer, L.M., Schinko, T., Surminski, S., Linnerooth-Bayer, J., Eds.; Springer: Cham, Switzerland, 2019; pp. 221–236.
3. Lavorel, S. Plant functional effects on ecosystem services. *J. Ecol.* **2013**, *101*, 4–8. [[CrossRef](#)]

4. Hillman, J.R.; Lundquist, C.J.; Thrush, S.F. The challenges associated with connectivity in ecosystem processes. *Front. Mar. Sci.* **2018**, *5*, 364. [[CrossRef](#)]
5. Balvanera, P.; Pfisterer, A.B.; Buchmann, N.; He, J.S.; Nakashizuka, T.; Raffaelli, D.; Schmid, B. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* **2006**, *9*, 1146–1156. [[CrossRef](#)] [[PubMed](#)]
6. Loreau, M.; Naeem, S.; Inchausti, P.; Bengtsson, J.; Grime, J.P.; Hector, A.; Wardle, D.A. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* **2001**, *294*, 804–808. [[CrossRef](#)]
7. Hanisch, M.; Schweiger, O.; Cord, A.F.; Volk, M.; Knapp, S. Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands. *J. Appl. Ecol.* **2020**, *57*, 1535–1550. [[CrossRef](#)]
8. Birkhofer, K.; Andersson, G.; Bengtsson, J.; Bommarco, R.; Dänhardt, J.; Ekbom, B.; Ekroos, J.; Hahn, T.; Hedlund, K.; Jönsson, A.; Lindborg, R.; Olsson, O.; Rader, R.; Rusch, A.; Stjernman, M.; Williams, A.; Smith, H. Relationships between multiple biodiversity components and ecosystem services along a landscape complexity gradient. *Biol. Conserv.* **2018**, *218*, 247–253. [[CrossRef](#)]
9. Maestre, F.T.; Castillo-Monroy, A.P.; Bowker, M.A.; Ochoa-Hueso, R. Species richness effects on ecosystem multifunctionality depend on evenness, composition and spatial pattern. *J. Ecol.* **2012**, *100*, 317–330. [[CrossRef](#)]
10. Gamfeldt, L.; Hillebrand, H.; Jonsson, P.R. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* **2008**, *89*, 1223–1231. [[CrossRef](#)]
11. Mouillot, D.; Villéger, S.; Scherer-Lorenzen, M.; Mason, N.W. Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE* **2011**, *6*, e17476. [[CrossRef](#)]

12. Luo, Y.H.; Cadotte, M.W.; Burgess, K.S.; Liu, J.; Tan, S.L.; Zou, J.Y.; Xu, K.; Li, D.Z.; Gao, L.M. Greater than the sum of the parts: How the species composition in different forest strata influence ecosystem function. *Ecol. Lett.* **2019**, *22*, 1449–1461. [[CrossRef](#)]
13. Gross, N.; Bagousse-Pinguet, Y.L.; Liancourt, P.; Berdugo, M.; Gotelli, N.J.; Maestre, F.T. Functional trait diversity maximizes ecosystem multifunctionality. *Nat. Ecol. Evol.* **2017**, *1*, 0132. [[CrossRef](#)] [[PubMed](#)]
14. Violle, C.; Navas, M.L.; Vile, D.; Kazakou, E.; Fortunel, C.; Hummel, I.; Garnier, E. Let the concept of trait be functional! *Oikos* **2007**, *116*, 882–892. [[CrossRef](#)]
15. Nock, C.A.; Vogt, R.J.; Beisner, B.E. Functional traits. In *eLS*; John Wiley & Sons, Ltd.: Chichester, UK, 2016; pp. 1–8. [[CrossRef](#)]
16. Adler, P.B.; Salguero-Gómez, R.; Compagnoni, A.; Hsu, J.S.; Ray-Mukherjee, J.; Mbeau-Ache, C.; Franco, M. Functional traits explain variation in plant life history strategies. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 740–745. [[CrossRef](#)] [[PubMed](#)]
17. Chaturvedi, R.K.; Tripathi, A.; Raghubanshi, A.S.; Singh, J.S. Functional traits indicate a continuum of tree drought strategies across a soil water availability gradient in a tropical dry forest. *For. Ecol. Manag.* **2021**, *482*, 118740. [[CrossRef](#)]
18. Feizabadi, M.F.; Tahmasebi, P.; Broujeni, E.A.; Ebrahimi, A.; Omidipour, R. Functional diversity, functional composition and functional β diversity drive aboveground biomass across different bioclimatic rangelands. *Basic Appl. Ecol.* **2021**, *52*, 68–81. [[CrossRef](#)]
19. Vargas-Hernández, J.G.; Zdunek-Wielgołaska, J. Urban green infrastructure as a tool for controlling the resilience of urban sprawl. *Environ. Dev. Sustain.* **2021**, *23*, 1335–1354. [[CrossRef](#)]
20. Hanif, M.; Yu, Q.; Rao, X.; Shen, W. Disentangling the contributions of plant taxonomic and functional diversities in shaping aboveground biomass of a restored forest landscape in Southern China. *Plants* **2019**,

- 8, 612. [[CrossRef](#)]
21. Zhu, J.; Jiang, L.; Zhang, Y. Relationships between functional diversity and aboveground biomass production in the Northern Tibetan alpine grasslands. *Sci. Rep.* **2016**, *6*, 34105. [[CrossRef](#)]
 22. Finegan, B., Peña-Claros, M., de Oliveira, A.; Ascarrunz, N., Bret-Harte, M., Carreño-Rocabado, G., Casanoves, F., Díaz, S.; Eguiguren Velepucha, P., Fernandez, F., Licona, J., Lorenzo, L.; Salgado Negret, B.; Vaz, M.; Poorter, L. 2014. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology*, *103*(1), pp.191-201. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *J. Ecol.* **2015**, *103*, 191–201. [[CrossRef](#)]
 23. Huang, X.; Su, J.; Li, S.; Liu, W.; Lang, X. Functional diversity drives ecosystem multifunctionality in a *Pinus yunnanensis* natural secondary forest. *Sci. Rep.* **2019**, *9*, 6979. [[CrossRef](#)] [[PubMed](#)]
 24. Bu, W.; Huang, J.; Xu, H.; Zang, R.; Ding, Y.; Li, Y.; Li, Y.; Lin, M.; Wang, J.; Zhang, C. Plant functional traits are the mediators in regulating effects of abiotic site conditions on aboveground carbon stock-evidence from a 30 ha tropical forest plot. *Front. Plant Sci.* **2019**, *9*, 1958. [[CrossRef](#)] [[PubMed](#)]
 25. Fyllas, N.M.; Michelaki, C.; Galanidis, A.; Evangelou, E.; Zaragoza-Castells, J.; Dimitrakopoulos, P.G.; Tsadilas, C.; Arianoutsou, M.; Lloyd, J. Functional trait variation among and within species and plant functional types in mountainous mediterranean forests. *Front. Plant Sci.* **2020**, *11*, 212. [[CrossRef](#)]
 26. Westoby, M.; Falster, D.S.; Moles, A.T.; Vesk, P.A.; Wright, I.J. Plant ecological strategies: Some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* **2002**, *33*, 125–159. [[CrossRef](#)]
 27. Díaz, S.; Kattge, J.; Cornelissen, J.H.; Wright, I.J.; Lavorel, S.; Dray, S.; Reu, B.; Kleyer, M.; Wirth, C.; Prentice, I.C.; et al. The global spectrum of plant form and function. *Nature* **2016**, *529*, 167–171. [[CrossRef](#)]

28. Diaz, S.; Cabido, M. Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* **2001**, *16*, 646–655. [[CrossRef](#)]
29. Reich, P.B. The world-wide ‘fast–slow’ plant economics spectrum: A traits manifesto. *J. Ecol.* **2014**, *102*, 275–301. [[CrossRef](#)]
30. de la Riva, E.G.; Prieto, I.; Villar, R. The leaf economic spectrum drives leaf litter decomposition in Mediterranean forests. *Plant Soil* **2019**, *435*, 353–366. [[CrossRef](#)]
31. Conti, G.; Díaz, S. Plant functional diversity and carbon storage—an empirical test in semi-arid forest ecosystems. *J. Ecol.* **2013**, *101*, 18–28. [[CrossRef](#)]
32. Laureto, L.M.O.; Cianciaruso, M.V.; Samia, D.S.M. Functional diversity: An overview of its history and applicability. *Nat. Conserv.* **2015**, *13*, 112–116. [[CrossRef](#)]
33. de la Riva, E.G.; Marañón, T.; Violle, C.; Villar, R.; Pérez-Ramos, I.M. Biogeochemical and ecomorphological niche segregation of Mediterranean woody species along a local gradient. *Front. Plant Sci.* **2017**, *8*, 1242. [[CrossRef](#)] [[PubMed](#)]
34. Lazarova, S.; Coyne, D.; Rodríguez, M.G.; Peteira, B.; Ciancio, A. Functional diversity of soil nematodes in relation to the impact of agriculture—A review. *Diversity* **2021**, *13*, 64. [[CrossRef](#)]
35. Valladares, F.; Bastias, C.C.; Godoy, O.; Granda, E.; Escudero, A. Species coexistence in a changing world. *Front. Plant Sci.* **2015**, *6*, 866. [[CrossRef](#)] [[PubMed](#)]
36. De Bello, F.; Lavorel, S.; Díaz, S.; Harrington, R.; Cornelissen, J.H.; Bardgett, R.D.; Matty, P.B.; Cipriotti, P.; Feld, C.K.; Hering, D.; Martins da Silva, P., Potts, S., Sandin, L., Sousa, J., Storkey, J., Wardle, D. and Harrison, P. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers. Conserv.* **2010**, *19*, 2873–2893. [[CrossRef](#)]
37. Birkhofer, K.; Fliessbach, A.; Gavín-Centol, M.P.; Hedlund, K.;

- Ingimarsdóttir, M.; Jørgensen, H.B.; Kozjek, K.; Meyer, S.; Montserrat, M.; Moreno, S.S. Conventional agriculture and not drought alters relationships between soil biota and functions. *Sci. Rep.* **2021**, *11*, 23975. [[CrossRef](#)]
38. Birkhofer, K.; Smith, H.G.; Weisser, W.W.; Wolters, V.; Gossner, M.M. Land-use effects on the functional distinctness of arthropod communities. *Ecography* **2015**, *38*, 889–900. [[CrossRef](#)]
39. Jayathilake, H.M.; Prescott, G.W.; Carrasco, L.R.; Rao, M.; Symes, W.S. Drivers of deforestation and degradation for 28 tropical conservation landscapes. *Ambio* **2021**, *50*, 215–228. [[CrossRef](#)]
40. Jung, M.; Rowhani, P.; Scharlemann, J.P. Impacts of past abrupt land change on local biodiversity globally. *Nat. Commun.* **2019**, *10*, 5474. [[CrossRef](#)]
41. Acheampong, E.O.; Macgregor, C.J.; Sloan, S.; Sayer, J. Deforestation is driven by agricultural expansion in Ghana's forest reserves. *Sci. Afr.* **2019**, *5*, e00146. [[CrossRef](#)]
42. Symes, W.S.; Edwards, D.P.; Miettinen, J.; Rheindt, F.E.; Carrasco, L.R. Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. *Nat. Commun.* **2018**, *9*, 4052. [[CrossRef](#)]
43. Oduro, K.A.; Mohren, G.M.J.; Pena-Claros, M.; Kyereh, B.; Arts, B. Tracing forest resource development in Ghana through forest transition pathways. *Land Use Policy* **2015**, *48*, 63–72. [[CrossRef](#)]
44. Damptey, F.G.; de la Riva, E.G.; Birkhofer, K. 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. *Front. For. Glob. Chang.* **2021**, *4*, 47. [[CrossRef](#)]
45. Damptey, F.G.; Birkhofer, K.; Nsiah, P.K.; de la Riva, E.G. Soil properties and biomass attributes in a former gravel mine area after two decades of forest restoration. *Land* **2020**, *9*, 209. [[CrossRef](#)]

46. Sharma, S.; MacKenzie, R.A.; Tieng, T.; Soben, K.; Tulyasuwan, N.; Resanond, A.; Blate, G.; Litton, C.M. The impacts of degradation, deforestation and restoration on mangrove ecosystem carbon stocks across Cambodia. *Sci. Total Environ.* **2020**, *706*, 135416. [[CrossRef](#)] [[PubMed](#)]
47. Bernal, B.; Murray, L.T.; Pearson, T.R. Global carbon dioxide removal rates from forest landscape restoration activities. *Carbon Balance Manag.* **2018**, *13*, 22. [[CrossRef](#)] [[PubMed](#)]
48. Aponte, C.; García, L.V.; Marañón, T. Tree species effects on nutrient cycling and soil biota: A feedback mechanism favouring species coexistence. *For. Ecol. Manag.* **2013**, *309*, 36–46. [[CrossRef](#)]
49. Pérez-Ramos, I.M.; Roumet, C.; Cruz, P.; Blanchard, A.; Autran, P.; Garnier, E. Evidence for a 'plant community economics spectrum' driven by nutrient and water limitations in a Mediterranean rangeland of southern France. *J. Ecol.* **2012**, *100*, 1315–1327. [[CrossRef](#)]
50. Hawthorne, W.D.N.; Gyakari, N. *Photoguide for the Forest Trees of Ghana: A Tree-Spotter's Field Guide for Identifying the Largest Trees*; Oxford Forestry Institute—Department of Plant Sciences: Oxford, UK, 2006.
51. Gatti, R.C.; Castaldi, S.; Lindsell, J.A.; Coomes, D.A.; Marchetti, M.; Maesano, M.; Di Paola, A.; Paparella, F.; Valentini, R. The impact of selective logging and clearcutting on forest structure, tree diversity and above-ground biomass of African tropical forests. *Ecol. Res.* **2015**, *30*, 119–132. [[CrossRef](#)]
52. Chave, J.; Réjou-Méchain, M.; Búrquez, A.; Chidumayo, E.; Colgan, M.S.; Delitti, W.B.; Duque, A.; Eid, T.; Fearnside, P.M.; Goodman, R.C.; Henry, M.; Martínez-Yrizar, A.; Mugasha, W.; Muller-Landau, H.; Mencuccini, M.; Nelson, B.; Ngomanda, A.; Nogueira, E.; Ortiz-Malavassi, E.; Pélissier, R.; Ploton, P.; Ryan, C.; Saldarriaga, J.; Vieilledent, G. Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Biol.* **2014**, *20*, 3177–3190. [[CrossRef](#)]

53. Zanne, A.E.; Lopez-Gonzalez, G.; Coomes, D.A.; Ilic, J.; Jansen, S.; Lewis, S.L.; Miller, R.B.; Swenson, N.G.; Wiemann, M.C.; Chave, J. Global Wood Density Database. Dryad Digital Repository. 2009. Available online: <https://datadryad.org/stash/dataset/doi:10.5061/dryad.234> (accessed on 28 August 2021).
54. Lewis, S.L.; Sonké, B.; Sunderland, T.; Begne, S.K.; Lopez-Gonzalez, G.; van der Heijden, G.M.; Philips, O.L.; Affum-Baffoe, K.; Baker, T.R.; Banin, L.; Bastin, J.; Beeckman, H.; Boeckx, P.; Bogaert, J.; De Cannière, C.; Chezeaux, E.; Clark, C.; Collins, M.; Djagbletey, G.; Djuikouo, M.; Droissart, V.; Doucet, J.; Ewango, C.; Fauset, S.; Feldpausch, T.; Foli, E.; Gillet, J.; Hamilton, A.; Harris, D.; Hart, T.; de Haulleville, T.; Hladik, A.; Hufkens, K.; Huygens, D.; Jeanmart, P.; Jeffery, K.; Kearsley, E.; Leal, M.; Lloyd, J.; Lovett, J.; Makana, J.; Malhi, Y.; Marshall, A.; Ojo, L.; Peh, K.; Pickavance, G.; Poulsen, J.; Reitsma, J.; Sheil, D.; Simo, M.; Steppe, K.; Taedoumg, H.; Talbot, J.; Taplin, J.; Taylor, D.; Thomas, S.; Toirambe, B.; Verbeeck, H.; Vleminckx, J.; White, L.; Willcock, S.; Woell, H.; Zemagho, L. Above-ground biomass and structure of 260 African tropical forests. *Philos. Trans. R. Soc. B Biol. Sci.* **2013**, *368*, 20120295. [[CrossRef](#)]
55. Brockerhoff, E.G.; Barbaro, L.; Castagneyrol, B.; Forrester, D.I.; Gardiner, B.; González-Olabarria, J.R.; Lyver, P.O.; Meurisse, N.; Oxbrough, A.; Taki, H.; Thompson, I.; van der Plas, F.; Jactel, H.; Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodivers. Conserv.* **2017**, *26*, 3005–3035. [[CrossRef](#)]
56. Keuskamp, J.A.; Dingemans, B.J.; Lehtinen, T.; Sarneel, J.M.; Hefting, M.M. Tea Bag Index: A novel approach to collect uniform decomposition data across ecosystems. *Methods Ecol. Evol.* **2013**, *4*, 1070–1075. [[CrossRef](#)]
57. Kattge, J.; Diaz, S.; Lavorel, S.; Prentice, I.C.; Leadley, P.; Bönisch, G.; Garnier, E.; Westoby, M.; Reich, P.B.; Wright, I.J.; Cornelissen, J.; Violle, C.; Harrison, S.; van Bodegom, P.; Reichstein, M.; Enquist, B.;

- Soudzilovskaia, N.; Ackerly, D.; Anand, M.; Atkin, O.; Bahn, M.; Taker, T.; Baldocchi, D.; Bekker, R.; Blanco, C.; Blonder, B.; Bond, W.; Bradstock, R.; Bunker, D.; Casanoves, F.; Cavender-Bares, J.; Chambers, J.; Chapin III, F.; Chave, J.; Coomes, D.; Cornwell, W.; Craine, J.; Dobrin, B.; Duarte, I.; Durka, W.; Elser, J.; Esser, G.; Estiarte, M.; Fagan, W.; Fang, J.; Fernández-Méndez, F.; Fidelis, A.; Finegan, B.; Flores, O.; Ford, H.; Frank, D.; Freschet, G.; Fyllas, N.; Gallagher, R.; Green, W.; Gutierrez, A.; Hickler, T.; Higgins, S.; Hodgson, J.; Jalili, A.; Jansen, S.; Joly, C.; Kerkhoff, A.; Kirkup, D.; Kitajima, K.; Kleyer, M.; Klotz, S.; Knops, J.; Kramer, K.; Kühn, I.; Kurokawa, H.; Laughlin, D.; Lee, T.; Leishman, M.; Lens, F.; Lenz, T.; Lewis, S.; Lloyd, J.; Llusià, J.; Louault, F.; Ma, S.; Mahecha, M.; Manning, P.; Massad, T.; Medlyn, B.; Messier, J.; Moles, A.; Müller, S.; Nadrowski, K.; Naeem, S.; Niinemets, Ü.; Nöllert, S.; Nüske, A.; Ogaya, R.; Oleksyn, J.; Onipchenko, V.; Onoda, Y.; Ordoñez, J.; Overbeck, G.; Ozinga, W.; Patiño, S.; Paula, S.; Pausas, J.; Peñuelas, J.; Phillips, O.; Pillar, V.; Poorter, H.; Poorter, I.; Poschlod, P.; Prinzing, A.; Proulx, R.; Rammig, A.; Reinsch, S.; Reu, B.; Sack, I.; Salgado-Negret, B.; Sardans, J.; Shiodera, S.; Shipley, B.; Siefert, A.; Sosinski, E.; Soussana, J.; Swaine, E.; Swenson, N.; Thompson, K.; Thornton, P.; Waldram, M.; Weiher, E.; White, M.; White, S.; Wright, S.; Yguel, B.; Zaehle, S.; Zanne, A.; Wirth, C. 2011.. TRY—A global database of plant traits. *Glob. Chang. Biol.* **2011**, *17*, 2905–2935. [[CrossRef](#)]
58. Rueden, C.T.; Schindelin, J.; Hiner, M.C.; DeZonia, B.E.; Walter, A.E.; Arena, E.T.; Eliceiri, K.W. ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinform.* **2017**, *18*, 529. [[CrossRef](#)]
59. Glozer, K. Protocol for Leaf Image Analysis—Surface Area. 2008. Available online: <http://ucanr.edu/sites/fruittree/files/49325.pdf> (accessed on 17 September 2021).
60. Perez-Harguindeguy, N.; Diaz, S.; Garnier, E.; Lavorel, S.; Poorter, H.; Jaureguiberry, P.; Bret-Harte, S.; Cornwell, W.K.; Craine, J.M.; Gurvich, D.E.; Urcelay, C.; Veneklaas, E.; Reich, P.; Poorter, L.; Wright, I.; Ray, P.;

- Enrico, L.; Pausas, J.; de Vos, A.; Buchmann, N.; Funes, G.; Quétier, F.; Hodgson, J.; Thompson, K.; Morgan, H.; ter Steege, H.; Sack, L.; Blonder, B.; Poschlod, P.; Vaieretti, M.; Conti, G.; Staver, A.; Aquino, S.; Cornelissen, J. Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **2016**, *64*, 715–716. [[CrossRef](#)]
61. Liu, M.; Wang, Z.; Li, S.; Lü, X.; Wang, X.; Han, X. Changes in specific leaf area of dominant plants in temperate grasslands along a 2500-km transect in northern China. *Sci. Rep.* **2017**, *7*, 10780. [[CrossRef](#)] [[PubMed](#)]
62. Prado, J.; Schiavini, I.; Vale, V.; Lopes, S.; Arantes, C.; Oliveira, A.P. Functional leaf traits of understory species: Strategies to different disturbance severities. *Braz. J. Biol.* **2015**, *75*, 339–346. [[CrossRef](#)]
63. Zhang, J.; He, N.; Liu, C.; Xu, L.; Chen, Z.; Li, Y.; Wang, R.; Yu, G.; Sun, W.; Xiao, C.; Chen, H.; Reich, P. Variation and evolution of C: N ratio among different organs enable plants to adapt to N-limited environments. *Glob. Chang. Biol.* **2020**, *26*, 2534–2543. [[CrossRef](#)] [[PubMed](#)]
64. Xu, X.; Yang, G.; Yang, X.; Li, Z.; Feng, H.; Xu, B.; Zhao, X. Monitoring ratio of carbon to nitrogen (C/N) in wheat and barley leaves by using spectral slope features with branch-and-bound algorithm. *Sci. Rep.* **2018**, *8*, 10034. [[CrossRef](#)] [[PubMed](#)]
65. Zou, Y.; Sang, W.; Bai, F.; Brennan, E.; Diekman, M.; Liu, Y.; Li, L.; Marples, A.; Shi, H.; Sui, Z.; Sun, X.; Wang, C.; Wang, X.; Warren-Thomas, E.; Yang, X.; Yu, Z.; Axmacher, J. Large-scale α -diversity patterns in plants and ground beetles (Coleoptera: Carabidae) indicate a high biodiversity conservation value of China's restored temperate forest landscapes. *Divers. Distrib.* **2019**, *25*, 1613–1624. [[CrossRef](#)]
66. Cornelissen, J.H.C.; Lavorel, S.; Garnier, E.; Díaz, S.; Buchmann, N.; Gurvich, D.E.; Reich, P.B.; ter Steege, H.; Morgan, H.D.; van der Heijden, M.G.A.; et al. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* **2003**,

- 51, 335–380. [[CrossRef](#)]
67. Moles, A.T.; Westoby, M. Seed size and plant strategy across the whole life cycle. *Oikos* **2006**, *113*, 91–105. [[CrossRef](#)]
68. Galán Díaz, J.; de la Riva, E.G.; Funk, J.L.; Vilà, M. Functional segregation of resource-use strategies of native and invasive plants across Mediterranean biome communities. *Biol. Invasions* **2021**, *23*, 253–266. [[CrossRef](#)]
69. Moles, A.T.; Warton, D.I.; Warman, L.; Swenson, N.G.; Laffan, S.W.; Zanne, A.E.; Pitman, A.; Hemmings, F.A.; Leishman, M.R. Global patterns in plant height. *J. Ecol.* **2009**, *97*, 923–932. [[CrossRef](#)]
70. Larjavaara, M.; Muller-Landau, H.C. Measuring tree height: A quantitative comparison of two common field methods in a moist tropical forest. *Methods Ecol. Evol.* **2013**, *4*, 793–801. [[CrossRef](#)]
71. Garnier, E.; Cortez, J.; Billès, G.; Navas, M.L.; Roumet, C.; Debussche, M.; Laurent, G.; Blanchard, A.; Aubry, D.; Bellmann, A.; Neill, C.; Toussaint, J. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **2004**, *85*, 2630–2637. [[CrossRef](#)]
72. De Bello, F.; Carmona, C.P.; Lepš, J.; Szava-Kovats, R.; Pärtel, M. Functional diversity through the mean trait dissimilarity: Resolving shortcomings with existing paradigms and algorithms. *Oecologia* **2016**, *180*, 933–940. [[CrossRef](#)]
73. Karadimou, E.K.; Kallimanis, A.S.; Tsiripidis, I.; Dimopoulos, P. Functional diversity exhibits a diverse relationship with area, even a decreasing one. *Sci. Rep.* **2016**, *6*, 35420. [[CrossRef](#)]
74. Laliberté, E.; Legendre, P. A distance-based framework for measuring from multiple traits functional diversity. *Ecology* **2010**, *91*, 299–305. [[CrossRef](#)]
75. Villéger, S.; Mason, N.W.; Mouillot, D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **2008**, *89*, 2290–2301. [[CrossRef](#)]

76. Rao, C.R. Diversity and dissimilarity coefficients: A unified approach. *Theor. Popul. Biol.* **1982**, *21*, 24–43. [[CrossRef](#)]
77. Botta-Dukát, Z. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.* **2005**, *16*, 533–540. [[CrossRef](#)]
78. Laughlin, D.C. The intrinsic dimensionality of plant traits and its relevance to community assembly. *J. Ecol.* **2014**, *102*, 186–193. [[CrossRef](#)]
79. Torchiano, M. *Effsize: Efficient Effect Size Computation (R Package)*; R Foundation for Statistical Computing: Vienna, Austria, 2016.
80. Blonder, B. Hypervolume concepts in niche-and trait-based ecology. *Ecography* **2018**, *41*, 1441–1455. [[CrossRef](#)]
81. Blonder, B.; Nogués-Bravo, D.; Borregaard, M.K.; Donoghue II, J.C.; Jørgensen, P.M.; Kraft, N.J.; Lessard, J.P.; Morueta-Holme, N.; Sandel, B.; Svenning, J.C.; Violle, C.; Rahbek, C.; Enquist, B. Linking environmental filtering and disequilibrium to biogeography with a community climate framework. *Ecology* **2015**, *96*, 972–985. [[CrossRef](#)]
82. Grueber, C.E.; Nakagawa, S.; Laws, R.J.; Jamieson, I.G. Multimodel inference in ecology and evolution: Challenges and solutions. *J. Evol. Biol.* **2011**, *24*, 699–711. [[CrossRef](#)]
83. Barton, K.; Barton, M.K. Package 'Mumin'; Version 1. 2015. Available online: <https://cran.r-project.org/package/MuMIn/MuMIn.pdf> (accessed on 17 September 2021).
84. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2019; ISBN 3-900051-07-0.
85. Moir, J.; Jordan, P.; Moot, D.; Lucas, R. Phosphorus response and optimum pH ranges of twelve pasture legumes grown in an acid upland New Zealand soil under glasshouse conditions. *J. Soil Sci. Plant Nutr.* **2016**, *16*, 438–460. [[CrossRef](#)]
86. Oliveras, I.; Bentley, L.; Fyllas, N.M.; Gvozdevaite, A.; Shenkin, A.F.; Peprah, T.; Morandi, P.; Peixoto, K.S.; Boakye, M.; Adu-Bredu, S.;

- Schwantes Marimon, B.; Marimon Junior, B.; Salinas, N.; Martin, R.; Asner, G.; Díaz, S.; Enquist, B.; Malhi, Y. The influence of taxonomy and environment on leaf trait variation along tropical abiotic gradients. *Front. For. Glob. Chang.* **2020**, *3*, 18. [[CrossRef](#)]
87. de la Riva, E.G.; Pérez-Ramos, I.M.; Tosto, A.; Navarro-Fernández, C.M.; Olmo, M.; Marañón, T.; Villar, R. Disentangling the relative importance of species occurrence, abundance and intraspecific variability in community assembly: A trait-based approach at the whole-plant level in Mediterranean forests. *Oikos* **2016**, *125*, 354–363. [[CrossRef](#)]
88. Wright, I.J.; Reich, P.B.; Westoby, M.; Ackerly, D.D.; Baruch, Z.; Bongers, F.; Cavender-Bares, J.; Chapin, T.; Cornelissen, J.H.C.; Diemer, M.; Flexas, J.; Garnier, E.; Groom, P.; Gulias, J.; Hikosaka, K.; Lamont, B.; Lee, T.; Lee, W.; Lusk, C.; Midgley, J.; Navas, M.; Niinemets, Ü.; Oleksyn, J.; Osada, N.; Poorter, H.; Poot, P.; Prior, L.; Pyankov, V.; Roumet, C.; Thomas, S.; Tjoelker, M.; Veneklaas, E.; Villar, R. The worldwide leaf economics spectrum. *Nature* **2004**, *428*, 821–827. [[CrossRef](#)] [[PubMed](#)]
89. de la Riva, E.G.; Violle, C.; Pérez-Ramos, I.M.; Marañón, T.; Navarro-Fernández, C.M.; Olmo, M.; Villar, R. A multidimensional functional trait approach reveals the imprint of environmental stress in Mediterranean woody communities. *Ecosystems* **2018**, *21*, 248–262. [[CrossRef](#)]
90. Gvozdevaite, A.; Oliveras, I.; Domingues, T.F.; Peprah, T.; Boakye, M.; Afriyie, L.; Peixoto, K.S.; de Farias, J.; de Oliveira, E.A.; Farias, C.C.A.; et al. Leaf-level photosynthetic capacity dynamics in relation to soil and foliar nutrients along forest–Savanna boundaries in Ghana and Brazil. *Tree Physiol.* **2018**, *38*, 1912–1925. [[CrossRef](#)] [[PubMed](#)]
91. Neyret, M.; Bentley, L.P.; Oliveras, I.; Marimon, B.S.; Marimon-Junior, B.H.; Almeida de Oliveira, E.; Passos, F.B.; Ccoscco, R.C.; dos Santos, J.; Reis, S.M.; et al. Examining variation in the leaf mass per area of dominant species across two contrasting tropical gradients in light of

- community assembly. *Ecol. Evol.* **2016**, 6, 5674–5689. [[CrossRef](#)]
92. Sterck, F.; Markesteijn, L.; Schieving, F.; Poorter, L. Functional traits determine trade-offs and niches in a tropical forest community. *Proc. Natl. Acad. Sci. USA* **2011**, 108, 20627–20632. [[CrossRef](#)] [[PubMed](#)]
93. Cornelissen, J.H.C. A triangular relationship between leaf size and seed size among woody species: Allometry, ontogeny, ecology and taxonomy. *Oecologia* **1999**, 118, 248–255. [[CrossRef](#)]
94. Pérez-Ramos, I.M.; Gómez-Aparicio, L.; Villar, R.; García, L.V.; Maranon, T. Seedling growth and morphology of three oak species along field resource gradients and seed mass variation: A seedling age-dependent response. *J. Veg. Sci.* **2010**, 21, 419–437. [[CrossRef](#)]
95. Quero, J.L.; Villar, R.; Marañón, T.; Zamora, R.; Poorter, L. Seed-mass effects in four Mediterranean *Quercus* species (*Fagaceae*) growing in contrasting light environments. *Am. J. Bot.* **2007**, 94, 1795–1803. [[CrossRef](#)]
96. Moles, A.T.; Falster, D.S.; Leishman, M.R.; Westoby, M. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *J. Ecol.* **2004**, 92, 384–396. [[CrossRef](#)]
97. Moles, A.T.; Westoby, M. Seedling survival and seed size: A synthesis of the literature. *J. Ecol.* **2004**, 92, 372–383. [[CrossRef](#)]
98. Wright, S.J.; Stoner, K.E.; Beckman, N.; Corlett, R.T.; Dirzo, R.; Muller-Landau, H.C.; Nunez-Iturri, G.; Peres, C.A.; Wang, B.C. The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* **2007**, 39, 289–291. [[CrossRef](#)]
99. Opuni-Frimpong, E.; Gabienu, E.; Adusu, D.; Opuni-Frimpong, N.Y.; Dampney, F.G. Plant diversity, conservation significance, and community structure of two protected areas under different governance. *Trees For. People* **2021**, 4, 100082. [[CrossRef](#)]
100. Padmakumar, B.; Sreekanth, N.P.; Shanthiprabha, V.; Paul, J.; Sreedharan, K.; Augustine, T.; Jayasooryan, K.K.; Rameshan, M.;

- Mohan, M.; Ramasamy, E.V.; Thomas, A., 2018. Tree biomass and carbon density estimation in the tropical dry forest of Southern Western Ghats, India. *iForest-Biogeosci. For.* **2018**, *11*, 534. [[CrossRef](#)]
101. Schuldt, A.; Ebeling, A.; Kunz, M.; Staab, M.; Guimarães-Steinicke, C.; Bachmann, D.; Buchmann, N.; Durka, W.; Fichtner, A.; Fornoff, F.; Härdtle, W.; Hertzog, L.; Klein, A.; Roscher, C.; Schaller, J.; von Oheimb, G.; Weigelt, A.; Weisser, W.; Wirth, C.; Zhang, J.; Bruelheide, H.; Eisenhauer, N. Multiple plant diversity components drive consumer communities across ecosystems. *Nat. Commun.* **2019**, *10*, 65. [[CrossRef](#)] [[PubMed](#)]
102. Wenninger, E.J.; Inouye, R.S. Insect community response to plant diversity and productivity in a sagebrush–steppe ecosystem. *J. Arid Environ.* **2008**, *72*, 24–33. [[CrossRef](#)]
103. McColloch, J.W. The reciprocal relation of soil and insects. *Ecology* **1922**, *3*, 288–301. [[CrossRef](#)]
104. Gunstone, T.; Cornelisse, T.; Klein, K.; Dubey, A.; Donley, N. Pesticides and Soil Invertebrates: A Hazard Assessment. *Front. Environ. Sci.* **2021**, *9*, 122. [[CrossRef](#)]
105. Amprako, L.; Stenchly, K.; Wiehle, M.; Nyarko, G.; Buerkert, A. Arthropod Communities in Urban Agricultural Production Systems under Different Irrigation Sources in the Northern Region of Ghana. *Insects* **2020**, *11*, 488. [[CrossRef](#)]
106. Raven, P.H.; Wagner, D.L. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2002548117. [[CrossRef](#)]
107. Zhao, Z.H.; Hui, C.; He, D.H.; Li, B.L. Effects of agricultural intensification on ability of natural enemies to control aphids. *Sci. Rep.* **2015**, *5*, 8024. [[CrossRef](#)]
108. Schjoerring, J.K.; Cakmak, I.; White, P.J. Plant nutrition and soil fertility: Synergies for acquiring global green growth and sustainable

- development. *Plant Soil* **2019**, 434, 1–6. [[CrossRef](#)]
109. Chatzistathis, T.; Therios, I. How soil nutrient availability influences plant biomass and how biomass stimulation alleviates heavy metal toxicity in soils: The cases of nutrient use efficient genotypes and phytoremediators, respectively. In *Biomass Now-Cultivation and Utilization*; Matovic, D.M., Ed.; IntechOpen: Rijeka, Croatia, 2013; pp. 427–448.
110. Måren, I.E.; Sharma, L.N. Seeing the wood for the trees: Carbon storage and conservation in temperate forests of the Himalayas. *For. Ecol. Manag.* **2021**, 487, 119010. [[CrossRef](#)]
111. Kothandaraman, S.; Dar, J.A.; Sundarapandian, S.; Dayanandan, S.; Khan, M.L. Ecosystem-level carbon storage and its links to diversity, structural and environmental drivers in tropical forests of Western Ghats, India. *Sci. Rep.* **2020**, 10, 13444. [[CrossRef](#)] [[PubMed](#)]
112. Liu, C.L.; Kuchma, O.; Krutovsky, K.V. Mixed-species versus monocultures in plantation forestry: Development, benefits, ecosystem services and perspectives for the future. *Glob. Ecol. Conserv.* **2018**, 1, e00419. [[CrossRef](#)]
113. Heilpern, S.A.; Anujan, K.; Osuri, A.; Naeem, S. Positive correlations in species functional contributions drive the response of multifunctionality to biodiversity loss. *Proc. R. Soc. B* **2020**, 287, 20192501. [[CrossRef](#)]
114. Zirbel, C.R.; Bassett, T.; Grman, E.; Brudvig, L.A. Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. *J. Appl. Ecol.* **2017**, 54, 1070–1079. [[CrossRef](#)]
115. Manning, P.; van der Plas, F.; Soliveres, S.; Allan, E.; Maestre, F.T.; Mace, G.; Whittingham, M.J.; Fischer, M. Redefining ecosystem multifunctionality. *Nat. Ecol. Evol.* **2018**, 2, 427–436. [[CrossRef](#)]
116. Shen, Y.; Yu, S.; Lian, J.; Shen, H.; Cao, H.; Lu, H.; Ye, W. Tree aboveground carbon storage correlates with environmental gradients and functional diversity in a tropical forest. *Sci. Rep.* **2016**, 6, 25304. [[CrossRef](#)]

117. Cavanaugh, K.C.; Gosnell, J.S.; Davis, S.L.; Ahumada, J.; Boundja, P.; Clark, D.B.; Mugerwa, B.; Jansen, P.A.; O'Brien, T.G.; Rovero, F.; Sheil, D.; Vasquez, R.; Andelman, S. Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. *Glob. Ecol. Biogeogr.* **2014**, *23*, 563–573. [[CrossRef](#)]
118. Mensah, S.; Veldtman, R.; Assogbadjo, A.E.; Glèlè Kakai, R.; Seifert, T. Tree species diversity promotes aboveground carbon storage through functional diversity and functional dominance. *Ecol. Evol.* **2016**, *6*, 7546–7557. [[CrossRef](#)]
119. Tilman, D.; Isbell, F.; Cowles, J.M. Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol. Syst.* **2014**, *45*, 471–493. [[CrossRef](#)]
120. Campos, R.I.; Vasconcelos, H.L.; Ribeiro, S.P.; Neves, F.S.; Soares, J.P. Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. *Ecography* **2006**, *29*, 442–450. [[CrossRef](#)]
121. Marques, E.S.D.A.; Price, P.W.; Cobb, N.S. Resource abundance and insect herbivore diversity on woody fabaceous desert plants. *Environ. Entomol.* **2000**, *29*, 696–703. [[CrossRef](#)]
122. Dampney, F.G.; Frimpong, B.F.; Debrah, D.K.; Agro, P.P.; Wiafe, E.D. Vegetation attributes drive the taxonomic richness and functional composition of beetles and spiders in mountainous urban green spaces. *Energy Ecol. Environ.* **2022**, *7*, 1–13. [[CrossRef](#)]
123. Wein, A.; Bauhus, J.; Bilodeau-Gauthier, S.; Scherer-Lorenzen, M.; Nock, C.; Staab, M. Tree species richness promotes invertebrate herbivory on congeneric native and exotic tree saplings in a young diversity experiment. *PLoS ONE* **2016**, *11*, e0168751. [[CrossRef](#)] [[PubMed](#)]
124. Goulnik, J.; Plantureux, S.; They, M.; Baude, M.; Delattre, M.; van Reeth, C.; Villerd, J.; Michelot-Antalik, A. Floral trait functional diversity is related to soil characteristics and positively influences pollination function in semi-natural grasslands. *Agric. Ecosyst. Environ.* **2020**, *301*, 107033. [[CrossRef](#)]

125. Cadotte, M.W.; Carscadden, K.; Mirotchnick, N. Beyond species: Functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* **2011**, *48*, 1079–1087. [[CrossRef](#)]
126. Ola, A.; Lovelock, C.E. Decomposition of mangrove roots depends on the bulk density they grew in. *Plant Soil* **2021**, *460*, 177–187. [[CrossRef](#)]
127. Nosalewicz, A.; Lipiec, J. The effect of compacted soil layers on vertical root distribution and water uptake by wheat. *Plant Soil* **2014**, *375*, 229–240. [[CrossRef](#)]
128. Kozłowski, T.T. Soil compaction and growth of woody plants. *Scand. J. For. Res.* **1999**, *14*, 596–619. [[CrossRef](#)]
129. Blakely, J.K.; Neher, D.A.; Spongberg, A.L. Soil invertebrate and microbial communities, and decomposition as indicators of polycyclic aromatic hydrocarbon contamination. *Appl. Soil Ecol.* **2002**, *21*, 71–88. [[CrossRef](#)]
130. Dissanayaka, D.M.; Dhananjaya, V.P.; Kosgollegedara, E.J.; Karthigayini, S. Impact of Improved Aeration on Decomposition Rate of Enriched Compost. *Int. J. Trend Sci. Res. Dev.* **2021**, *5*, 852–857.
131. Ola, A.; Gauthier, A.R.; Xiong, Y.; Lovelock, C.E. The roots of blue carbon: Responses of mangrove stilt roots to variation in soil bulk density. *Biol. Lett.* **2019**, *15*, 20180866. [[CrossRef](#)] [[PubMed](#)]
132. Herrick, J.E.; Lal, R. Soil physical property changes during dung decomposition in a tropical pasture. *Soil Sci. Soc. Am. J.* **1995**, *59*, 908–912. [[CrossRef](#)]
133. Mensah, S.; van der Plas, F.; Noulèkoun, F. Do functional identity and divergence promote aboveground carbon differently in tropical semi-arid forests and savannas? *Ecosphere* **2021**, *12*, e03563. [[CrossRef](#)]
134. Le Bagousse-Pinguet, Y.; Soliveres, S.; Gross, N.; Torices, R.; Berdugo, M.; Maestre, F.T. Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 8419–8424. [[CrossRef](#)]

135. Grman, E.; Zirbel, C.R.; Bassett, T.; Brudvig, L.A. Ecosystem multifunctionality increases with beta diversity in restored prairies. *Oecologia* **2018**, *188*, 837–848. [[CrossRef](#)]
136. The Plant List. Version 1.1. 2013. Available online: <http://www.theplantlist.org/> (accessed on 1 January 2022).

Chapter V: Effects of post-mining forest restoration and alternative land-uses on ground-dwelling arthropods in Ghana

Resubmitted after revision in **Community Ecology**

Frederick Gyasi Dampsey^{1*}, El Aziz Djoudi¹, Klaus Birkhofer¹

¹ Department of Ecology, Brandenburg University of Technology, 03046
Cottbus, Senftenberg, Germany

frederickGyasi.Dampsey@b-tu.de (F.G.D.)

elaziz.djoudi@b-tu.de (E.A.D.)

klaus.birkhofer@b-tu.de (K.B.)

***Corresponding author**

Effects of post-mining forest restoration and alternative land-uses on ground-dwelling arthropods in Ghana

Frederick Gyasi Dampney*, El Aziz Djoudi, Klaus Birkhofer

Department of Ecology, Brandenburg University of Technology, 03046 Cottbus, Senftenberg, Germany

*Correspondence: FrederickGyasi.Dampney@b-tu.de

Abstract

In an Afrotropical region experiencing massive deforestation, restoration approaches should provide sustainable solutions for recovering biodiversity. Arthropods are a sensitive taxonomic group for habitat alteration by deforestation and can be good indicators for restoration studies. Ground-dwelling arthropods provide important ecosystem functions, such as predation or organic matter decomposition, thereby contributing to ecosystem functionality. The consequences of post-mining management on arthropods in the Afrotropical region remain understudied. We carried out a comprehensive sampling of ground-dwelling arthropods in the dry and wet seasons across four land-use types in the semi-deciduous forest zone of Ghana. We then analysed whether the specific tree communities, vegetation structure and seasonal differences affected arthropod communities in the restored post-mining forest compared to the dominant alternative land-use type (agroforestry plantation), a natural reference (natural forest) or an unmanaged former mining area (gravel mine). In total, 43364 arthropods were sampled and assigned to 78 taxonomic groups representing 14 order/sub-order, 28 beetle families, 25 spider families, 5 hunting guilds of spiders and 6 trophic groups of beetles. Overall, Araneae, Coleoptera, Hymenoptera and Orthoptera all had higher activity-densities in the wet season. The vegetation structure of the three land-use types with trees supported a greater overall activity-density of arthropods and a more diverse functional composition compared to the unmanaged gravel site. Pronounced variation between the dry and wet seasons further influenced the taxonomic and functional composition. The active forest restoration of this post-mining area is a promising approach to drive arthropod communities towards a comparable state observed in the natural forest.

Keywords: Afrotropical, arthropod community, functional composition, post-mining, vegetation complexity

Introduction

Arthropods play a key role in ecosystem functioning and provide important ecosystem services for human societies, including local communities in Western Africa (Isaacs et al., 2009; Culliney, 2013; Høye & Culler, 2018; Sagi & Hawlena, 2021). Between 5 and 10 million terrestrial arthropod species have been described worldwide (Ødegaard, 2000; Novotny et al., 2002; Stork, 2018), of which up to 3.7 million species are found in the tropics (May, 2010). The Afrotropical region features a wide range of natural habitats with diverse plant and animal communities (Stuart et al., 1990), many of which are endemic to the region. In terms of ecosystem services provided by arthropods (Biondi et al., 2015; Dangles & Casas, 2019), pollination, nutrient regulation, soil formation and pest control contribute to human well-being (Rader et al., 2016; Schowalter, 2017; Birkhofer et al., 2018). Thereby, arthropods contribute to global food security (van der Sluijs & Vaage, 2016) and consequently reduce poverty (Dangles & Casas, 2019), as for example, predators (e.g., spiders) prey on herbivorous organisms, which could become pests on crops (Nyffeler et al., 2016).

Arthropod populations and diversity are threatened by human activities stemming from agricultural intensification, mining and land-use conversion or habitat loss (Birkhofer et al., 2015; Picanço et al., 2017; Seibold et al., 2019; Dampney et al., 2022a). Mining has been a crucial economic sector in many developing countries but comes with costs for biodiversity and interrupts the provision of several ecosystem services to human society (Schueler et al., 2011; Sonter et al., 2018; Ofosu et al., 2020; Asare et al., 2022). For instance, surface mining leads to the degradation of forests that would have otherwise provided habitat for pollinating or seed-dispersing arthropods, with consequences for local and global food security (Sonter et al., 2018). In addition, a shortage of productive land coupled with changing local and regional weather conditions because of land degradation and climate change leads to a decline in farm productivity and an increase in food insecurity globally (Ime & Ekong, 2015). Similarly, the removal of trees during mining eliminates the ability of forests to store carbon, with severe

implications for climate change (Ontl et al., 2020). Moreover, a land-use change that involves the conversion of a particular land-use type (e.g., natural forest) to alternative land use (e.g. agroforestry plantations) is known to result in a loss of arthropod biodiversity in some regions (e.g. Newbold, 2018). The high rate of conversion of tropical forests to other land uses is also anticipated to have consequences for both local and regional biodiversity, with cascading effects on other ecological processes (Schroeder et al., 2021). For instance, it is very obvious that the conversion of forests to agricultural lands or recreational parks affects arthropod diversity on a global scale (Perry et al., 2016; Millard et al., 2021), but the effect of restoring post-mining areas through restoration or agroforestry on arthropods is relatively unknown in Ghana and responses may differ among different taxonomic or functional arthropod groups. Restoration in Ghana sometimes takes the form of agroforestry, where economic and ecological valued tree species are interplanted with food crops to meet societal needs or enrichment planting to restore degraded forests (Dampney et al., 2021). Although several studies have discussed the devastating effects of land-use change on arthropods elsewhere in the world (e.g. Cardoso et al., 2020; Gagnarli et al., 2021), the consequences of land-use conversion and post-mining restoration in Ghana and Western Africa, in general, remain understudied.

In addition to the impact of land-use changes, pronounced seasonal differences will also affect the taxonomic and functional composition of arthropod communities (Wardhaugh et al., 2018). In Ghana, the two major seasons are based on the amount of precipitation, differences in temperature and the number of dry months (Owusu & Waylen, 2013). The characteristic rainfall in the wet season (April to July) should facilitate the emergence of arthropods from soil and the development of large patches of potential host plants (Basset et al., 2015). However, the dry season, with its long period of drought conditions, is accompanied by water stress-inducing physiological constraints and limited resource availability, thereby limiting the ability of arthropods to perform essential ecological functions and other services (Huberty & Denno, 2004).

To address the question of how post-mining restoration affects arthropod communities compared to a natural reference system, an alternative land use type and an unmanaged former mining area in the two major seasons in Ghana, we tested the following hypotheses: (i) land-use types with diverse tree communities, and heterogeneous vegetation structure (natural and restored forest) support a higher number of arthropod orders, functional groups and overall activity density than in agroforestry plantation and former mining area and (ii) the effect of land-use types on the taxonomic and functional composition of arthropods depends on the season with the strongest expected differences between land-use types with trees and agroforestry plantation and former mining area in the wet season.

Materials and methods

Study area

The studied land-use types include the following: 1.) an actively "restored forest" as restoration activity (Terchire restoration area; RF), 2.) an "agroforestry plantation" as an alternative land-use (Bosomkese forest reserve; AF), 3.) a "natural forest" as a natural reference, (Asukese forest reserve; NF) and 4.) an unmanaged "gravel site" as an unmanaged system (Terchire abandoned gravel mine site; GS). All land-use types lie in a semi-deciduous forest zone (SDFZ) and are located in the Ahafo and Bono regions of Ghana (Figure 1; Dampney et al., 2022b). The forest zone is characterised by a mean daily temperature of 20°C and annual precipitation ranging between 900 to 1500 mm (rainfall peaks between July and August; Dampney et al., 2021).

The RF is located in Terchire (7°14'4.78" N, 2°10'49.88" W), about 24 km from Sunyani, the Bono regional capital of Ghana. It was actively restored after gravel mining by planting leguminous cover crops (e.g., *Mucuna bracteata*, *Luffa egyptiaca*, *Pueraria phaseoloides*) and trees, both indigenous (e.g., *Morinda lucida* Benth, *Terminalia suberba* Engl. & Diels, *Albizia zygia* (DC) J. F. Machr, *Mangifera indica* L., *Ceiba pentandra* (L.) Gaertn.) and exotic (e.g., *Tectona grandis* L. f., *Cedrella odorata* L., *Senna siamia* (Lam.) H. S. Irwin & Barneby)

species after soil improvement and cover crops to provide essential ecosystem goods and services to local communities (Dampney et al., 2022b). The vertical profile of tree communities in RF is mainly uniform and characterised by upper canopy trees. The AF (7° 6'20.76" N, 2°15'22.64" W) is a degraded forest that has been subjected to agroforestry programs (food crops interplanted with trees) to supply both food and energy needs as well as environmental benefits to local communities. It is characterised by frequent annual wildfire events (Dampney et al., 2020). The NF (7° 9'13.72" N, 2°31'4.96" W) is a protected forest reserve under strict restrictions against anthropogenic activities. It is composed of native tree species, including *Celtis mildbraedii*, *Triplochiton scleroxylon*, *Cola gigantea*, *Nesogordonia papaverifera*. The vertical profile of tree communities in NF is a multi-layered structured with shrub layer, lower canopy, upper canopy and emerging trees. The GS is a four-hectare abandoned gravel mine (7°14'9.26"N, 2°9'36.13"W) located about 1.8 km from RF and colonised by the following invasive species; *Chromolaena odorata* and *Pennisetum purpureum* (Dampney et al., 2020). Table 1 provides an overview of selected vegetation attributes in all land-use types (Dampney et al., 2020, 2021).

Table 1 Vegetation structure (means and standard errors) of tree communities in the studied land-use types.

Vegetation attributes	Land-uses			
	Restored forest	Agroforestry plantation	Natural forest	Gravel site
Tree species (n/ha)	9 ± 1.7	7 ± 0.9	12 ± 0.9	1 ± 0.3
Tree abundance (n/ha)	30 ± 3.6	27 ± 2.9	23 ± 2.7	2 ± 0.4
Tree diameter (cm)	30.5 ± 4.7	38.5 ± 3.8	51.4 ± 5.4	9.2 ± 3.5
Basal area (m ² /ha)	3.0 ± 0.9	4.7 ± 0.4	6.9 ± 1.2	0.9 ± 0.3
Tree height (m)	13.3 ± 0.3	15.2 ± 0.8	14.3 ± 0.2	4.4 ± 1.7
Deadwood volume (m ³ /ha)	1740.2 ± 338	5816.7 ± 1209.0	7626.1 ± 2277.2	0.0 ± 0.0
Litter depth (cm)	2.8±0.1	2.1±0.1	3.1±0.1	0.0±0.0
Canopy openness (%)	19.2±1.4	20.2±0.9	12.7±0.7	91.4±0.9
Species composition	18% exotic, 82% native	6% exotic, 94% native	100% native	-
Dominant tree species	<i>leucaena</i> , <i>leucocephala</i> , <i>Senna siamea</i> , <i>Mangifera indica</i> , <i>Morinda lucida</i> , <i>Terminalia superba</i> , <i>Annona muricata</i> , <i>Albizia zygia</i> , <i>Blighia sapida</i>	<i>Ceiba pentandra</i> , <i>Triplochiton scleroxylon</i> , <i>Cedrela odorata</i> , <i>Terminalia superba</i> , <i>Cola gigantea</i> , <i>Mangifera indica</i> , <i>Dialium guineense</i> , <i>Microdesmis puberula</i> , <i>Cola nitida</i> , <i>Celtis mildbraedii</i> , <i>Albizia zygia</i> , <i>Alstonia boonei</i>	<i>Celtis mildbraedii</i> , <i>Triplochiton scleroxylon</i> , <i>Cola gigantea</i> , <i>Nesogordonia papaverifera</i> , <i>Celtis aldolfi-frider</i> , <i>Albizia zygia</i> , <i>Chrysophyllum albidum</i> , <i>Cola nitida</i> , <i>Tetrapleura tetraptera</i> , <i>Sterculia rhinopetala</i> , <i>Entandrophragma utile</i>	<i>Anacardium occidentale</i>

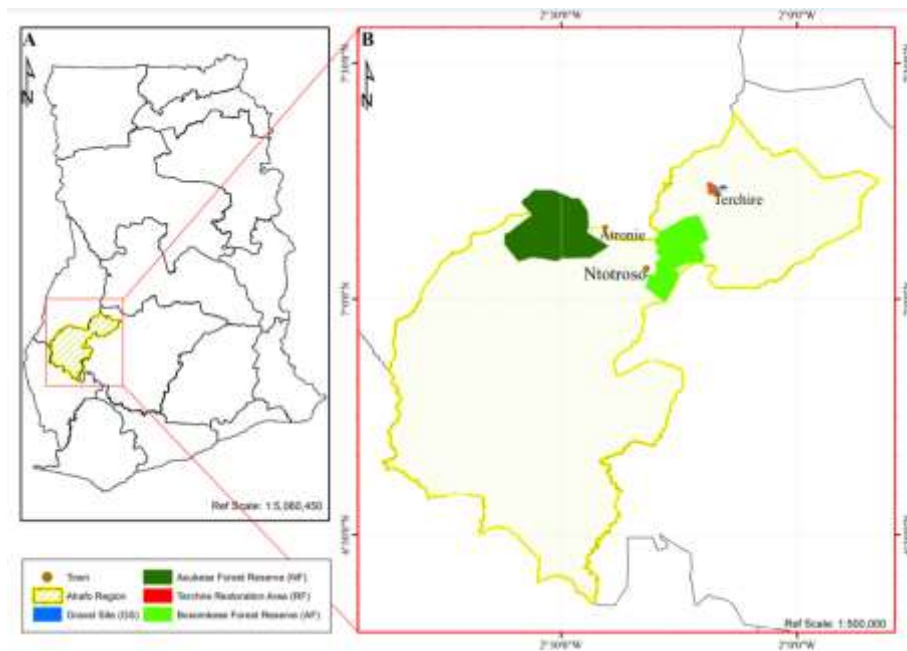


Figure 1 Map of Ghana (A) with the study region in Ghana and the studied land-use types (B)

Sampling design

The four land-use types were studied across both seasons (dry and wet) in the semi-deciduous forest zone (SDFZ) of Ghana. Each land-use was studied in eight replicate 20 × 20 m plots, resulting in 32 study plots. Basic vegetation attributes (Table 1) were surveyed and used to describe the major dendrological characteristics of each land-use type (see also Dampney et al., 2020, 2021). A standardised trapping method involving the use of pitfall traps was used to sample and estimate the activity density (A_D: number of samples caught divided by the sampling effort) of ground-dwelling arthropods based on their locomotory activities (Perner & Schueler, 2004; Greenslade, 1964).

Ground-dwelling arthropod communities were continuously sampled, with five pitfall traps in each plot being emptied weekly for 10 weeks in each sampling season. The first campaign was conducted in the dry season (January to March 2019), followed by the wet season campaign (June to August 2019). Pitfall traps were filled with a 50:50% mixture of propylene glycol and water, and all pitfall traps

were covered by small roofs to avoid dilution of the trap liquid by rain (Underwood & Quinn, 2010). Pitfall trap samples were stored in 70% ethanol and later sorted into taxonomic groups (order, suborder or family) according to available identification keys (for spiders; Dippenaar-Schoeman & Jocqué, 1997) and insects; Picker (2012). Individuals of the orders Coleoptera and Araneae were always sorted at the family level. The Coleoptera (beetle) families were subsequently classified into trophic groups (detritivores, herbivores, carnivores, and fungivores; some families cannot be assigned to one of those categories leading to the combined classes herbivores & detritivores and carnivores & detritivores; Lassau et al., 2005). The Araneae (spider) families were also classified into hunting guilds (sensing web, ground hunters, ambush hunters, other hunters and specialist spiders; Cardoso et al., 2011).

Data analyses

Arthropod community data for plots within each land-use type were pooled together and log transformed [$\log(x+1)$]. Activity density (A_D) of arthropods for land-use types and seasons was estimated based on the number of individuals sampled divided by the sampling effort (Greenslade, 1964).

A non-metric multidimensional scaling ordination (NMDS) based on Bray-Curtis similarities was created to visually represent the multivariate relationship within and between sampling plots of different land-use types and seasons. The goodness of fit of NMDS ordinations was evaluated using the 2-d stress value (Clarke et al., 2014). For the NMDS based on the taxonomic composition of all arthropods, vectors were superimposed for orders with Pearson correlation coefficients > 0.2 with axis scores. For the identification of Coleoptera and Araneae families and functional groups that were characteristic of land-use types or seasons, similarity percentage analysis (SIMPER) was used based on Bray-Curtis similarity and a cut-off value of 70% for the total contribution (Sommerfield & Clarke, 2013). Statistical analyses and visualisations were carried out with the Plymouth Routines in Multivariate Ecological Research (PRIMER vs 7; Clarke & Gorley,

2015) or R statistical computing software version 2.15.3 (R Core Team, 2019).

Results

Arthropod taxonomic composition

In total, 43364 arthropods were sampled and assigned to 78 taxonomic groups representing 14 order/sub-order (Appendix A), 28 beetle families (divided into 6 trophic groups), and 25 spider families (divided into 5 hunting guilds). The arthropod communities at the former gravel mine are unique for both seasons, followed by a gradient from the agroforestry plantation to the restored and the natural forest communities with increasing activity densities of Blattodea, Julida, Hymenoptera, Coleoptera and Araneae along that gradient independent of the season (Fig. 2). The restored forest plots have an intermediate position between the agroforestry plantation and the natural forest arthropod communities. Within land-use types, Hemiptera had a higher activity density in the dry season compared to the wet season. Blattodea and Julida had the highest activity density in the natural forest and were absent from the gravel site. Within land-use types, Orthoptera had a higher activity density in the wet season, and Polydesmida were only present in the wet season.

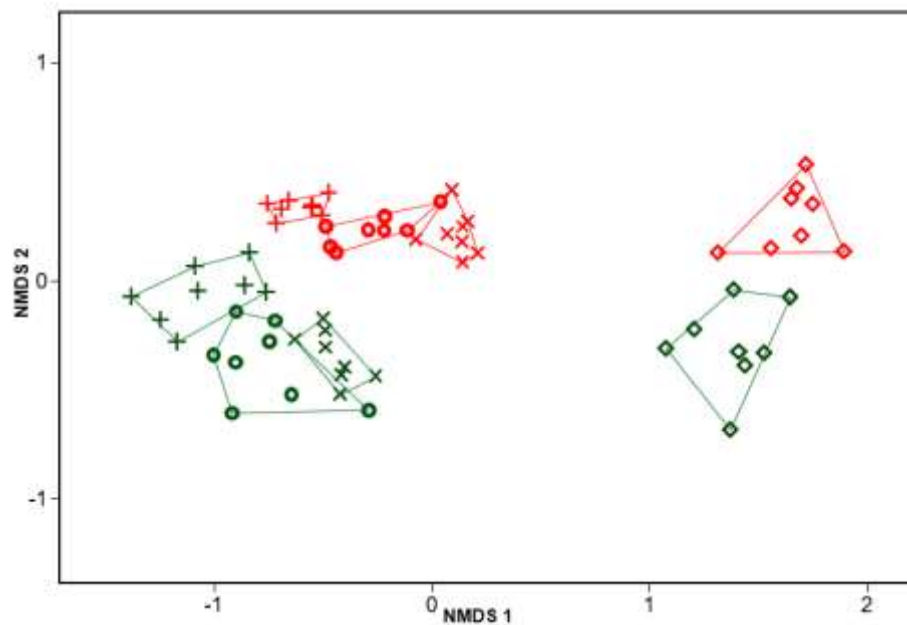


Figure 2 Non-metric multidimensional scaling ordination based on log-transformed ($\log(x+1)$) activity densities of arthropod orders or suborders and Bray-Curtis similarities between plots of different land-use types (\circ Restored forest, \times Agroforestry plantation, $+$ Natural forest, and \diamond Gravel site) and seasons (green = wet, red = dry). The 2-d stress value is 0.06. Symbols of each land-use type and season combination are connected by minimum spanning trees

Spider family composition

The total activity density of spiders was higher in NF (3.03) than RF (2.79), AF (1.59) and GS (1.35) and also higher in the wet (5.44) than in the dry season (3.32). The families Lycosidae, Salticidae and Zodariidae, dominated communities, amounting to more than 50% of all individuals in each of the four land-use types. Most families (e.g. Corinnidae, Ctenidae, Migidae, Zodariidae) had higher activity densities in the wet season, except Oxyopidae, which had a higher activity density in the dry season, and Lycosidae and Salticidae, which did not differ much between seasons (Fig. 3). Spider family composition showed a gradient from the dry season agroforestry plantation and the gravel site for both seasons towards the restored forest and the natural forest plots for both seasons. For spider communities, the wet season agroforestry plots hold an intermediate position between the restored and natural forest plots.

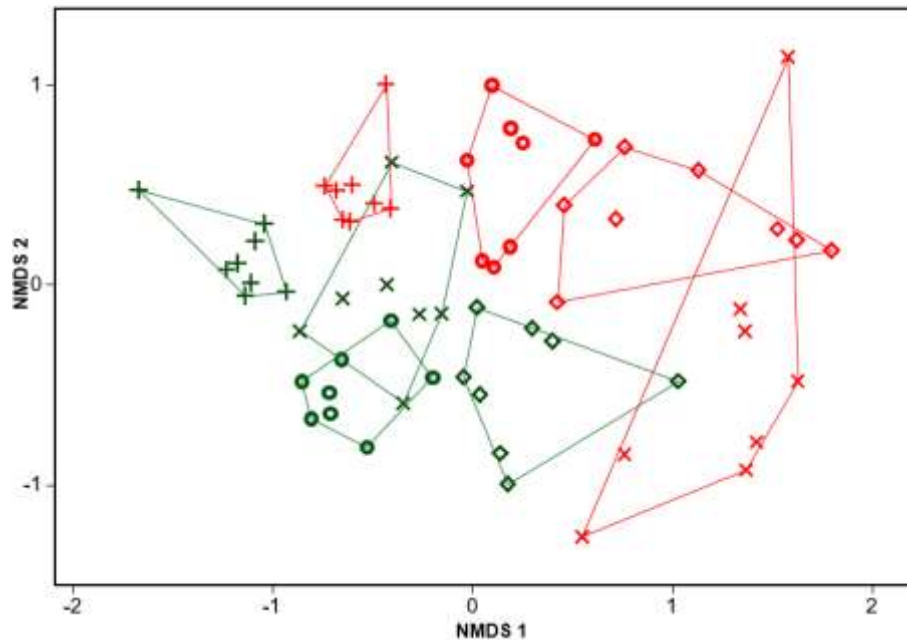


Figure 3 Non-metric multidimensional scaling ordination based on log-transformed ($\log(x+1)$) activity densities of spiders and Bray-Curtis similarities between plots of different land-use types (\circ Restored forest, \times Agroforestry plantation, $+$ Natural forest, and \diamond Gravel site) and seasons (green = wet, red = dry). The 2-d stress value is 0.19. Symbols of each land-use type and season combination are connected by minimum spanning trees

The average dissimilarity between the dry and wet season plots was 44% and was driven by a higher activity density of Salticidae, Zodariidae, Ctenidae, Corinnidae, Lycosidae and Cyrtacheniidae in the wet season (Table 2). In terms of dominance, the dry season plots were dominated by Lycosidae (28% of all individuals), Zodariidae (25%), Salticidae (15%) and Corinnidae (12%) and differed from wet season plots due to an even higher dominance of Lycosidae (52%) but lower dominance of Zodariidae (16%) and Salticidae (12%) in the wet season.

Table 2 Contribution of spider families to the dissimilarities in community composition between the wet and dry season plots based on similarity percentage analysis (SIMPER; AD = Average activity density, Diss. = Average Dissimilarity, SD = Standard Deviation, Contrib.% = Contribution percentage to overall dissimilarity, Cum. % = Cumulative contribution percentage).

Family	Wet AD	Dry AD	Diss.	Diss./SD	Contrib. %	Cum.%
Salticidae	1.83	1.52	6.89	1.49	15.83	15.83
Zodariidae	2.46	1.22	6.75	1.59	15.50	31.32
Ctenidae	1.60	0.76	5.66	1.47	12.99	44.31
Corinnidae	1.35	0.63	5.06	1.26	11.62	55.93
Lycosidae	2.83	2.70	4.30	1.43	9.88	65.81
Cyrtacheniidae	0.85	0.14	3.98	1.13	9.15	74.96

Spider hunting guilds

Ground hunters ($A_D = 4.13$) were the most dominant group across land-use types, followed by other hunters ($A_D = 2.61$), specialists ($A_D = 1.59$), sensing web ($A_D = 0.35$) and ambush hunters ($A_D = 0.07$). Ground hunters were more active in RF than GS, AF and NF (Fig. 4A). Sensing spiders were rather active in the AF than NF, RF and GS (Fig. 4B). Other hunters were also more active in NF than RF, AF and GS (Fig. 4C). For specialist's spiders, higher activity density was recorded for NF compared to RF, GS and AF (Fig. 4D).

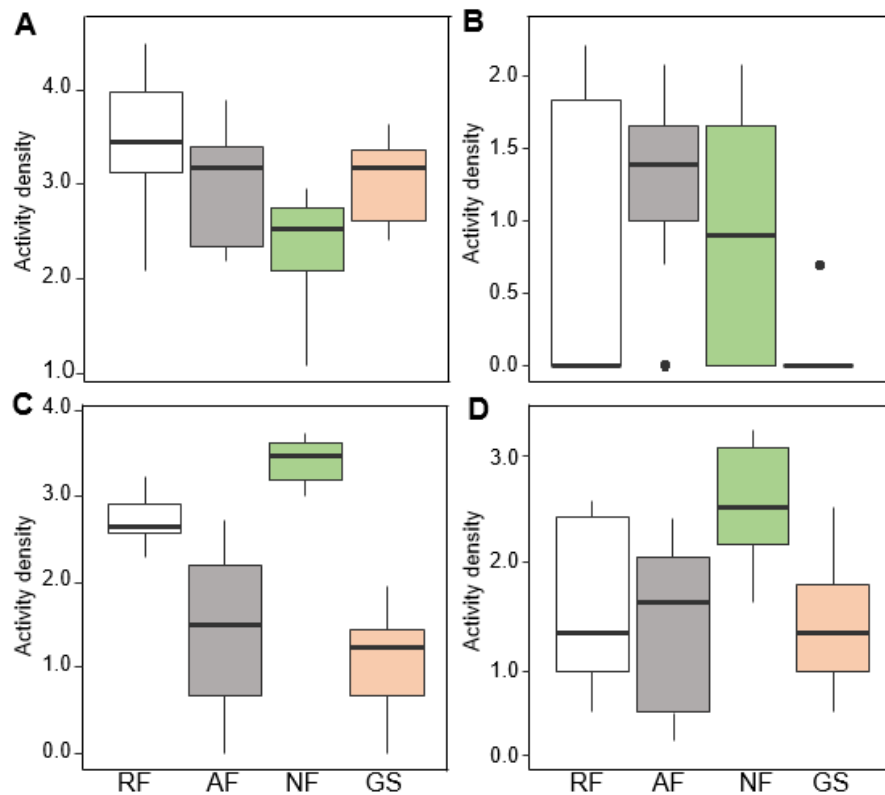


Figure 4 Box plots for activity densities in different hunting guilds (A, ground hunters; B, sensing web; C, other hunters and D, specialist spiders) between land-use types: RF, restored forest; AF, agroforestry plantation; NF, natural forest and GS, gravel site. Single points indicate outliers based on Median and Interquartile Deviation Method (IQD).

Beetle family composition

The taxonomic composition of beetle communities differed significantly between land-use types ($F_{3,27} = 14.52$; $p < 0.001$) and seasons ($F_{1,27} = 46.14$; $p < 0.001$). The differences between land-use types did depend on the season ($F_{3,27} = 10.80$; $p < 0.001$). Pairwise statistical comparisons indicated significant differences in family composition between beetle communities of the natural forest and the agroforestry plantation ($t = 4.41$, $p < 0.001$), restored forest ($t = 3.24$, $p < 0.001$), gravel site ($t = 4.50$, $p < 0.001$) and between the restored forest and the agroforestry plantation ($t = 2.02$, $p = 0.005$), gravel site ($t = 3.86$, $p < 0.001$) as well as between the agroforestry plantation and the gravel site ($t = 3.78$, $p < 0.001$).

Beetle communities at the former gravel mine were unique and more heterogeneous during the dry season than during the wet season, with a higher activity density of Elateridae at the gravel site plots (Fig. 5). The beetle communities in the wet season restored and natural forest plots resembled each other and were characterised by higher activity densities of Histeridae, Hydrophilidae and Staphylinidae. While beetle communities did not differ between the natural and restored forests in the wet season, they differed in the dry season. Beetle communities in the agroforestry plantation in the wet season resembled forest communities in the dry season more than other communities in habitats with trees in the wet season.

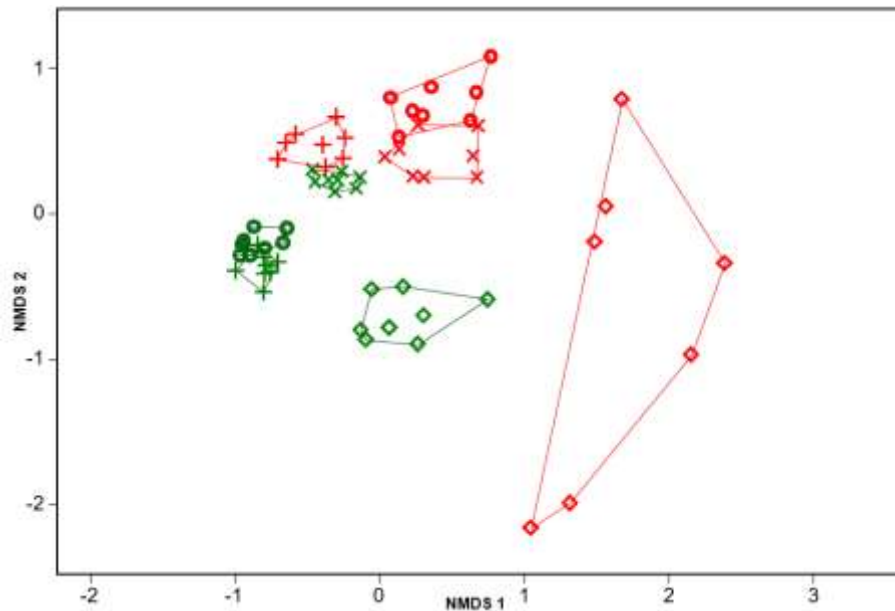


Figure 5 Non-metric multidimensional scaling ordination based on log-transformed ($\log(x+1)$) activity densities of beetles and Bray-Curtis similarities between plots of different land-use types (\circ Restored forest, \times Agroforestry plantation, $+$ Natural forest, and \diamond Gravel site) and seasons (green = wet, red = dry). The 2-d stress value is 0.13. Symbols of each land-use type and season combination are connected by minimum spanning trees

In terms of dominance, the dry season plots were dominated by Tenebrionidae (36% of all individuals), Nitidulidae (20%), Carabidae (10%) and Erotylidae (8%)

and differed from wet season plots by and even higher dominance by Scarabaeidae (26%) and Carabidae (22%) but lower dominance of Staphylinidae (13%), Nitidulidae (9%) and Cetonidae (7%). The average dissimilarity between the dry and wet season plots was 65% and was driven by a higher activity density of Scarabaeidae, Carabidae, Staphylinidae, Hydrophilidae, Histeridae, and Cetonidae in the wet season but a higher activity density of Tenebrionidae and Nitidulidae in the dry season (Table 3).

Table 3 Contribution of beetle families to the dissimilarities in community composition between the wet and dry season plots based on similarity percentage analysis (SIMPER; AD = Average activity density, Diss. = Average Dissimilarity, SD = Standard Deviation, Contrib.% = Contribution percentage to overall dissimilarity, Cum. % = Cumulative contribution percentage).

Family	Wet AD	Dry AD	Diss.	Diss./SD	Contrib.%	Cum.%
Scarabaeidae	3.47	0.94	9.86	1.58	15.06	15.06
Carabidae	2.95	0.97	7.69	1.59	11.76	26.82
Tenebrionidae	1.08	2.24	5.90	1.34	9.02	35.84
Staphylinidae	2.00	1.00	5.49	1.50	8.38	44.22
Hydrophilidae	1.66	0.19	5.11	0.91	7.81	52.03
Histeridae	1.46	0.10	4.69	1.09	7.17	59.20
Cetonidae	1.07	0.09	4.33	1.04	6.62	65.82
Nitidulidae	1.52	1.57	4.04	1.15	6.17	71.99

Beetle trophic groups

Based on the activity density of beetle trophic groups, the following order reflects their dominance across land-use types: detritivores (67%), carnivores (18%), herbivores (8%) and fungivores (7%). The activity density of detritivores ($F_{3,28} = 29.95$; $p < 0.001$), carnivores ($F_{3,28} = 13.76$; $p < 0.001$), herbivores ($F_{3,28} = 31.64$; $p < 0.001$), fungivores ($F_{3,28} = 46.14$; $p < 0.001$), herbivores & detritivores ($F_{3,28} = 33.34$; $p < 0.001$) and carnivores & detritivores ($F_{3,28} = 46.64$; $p < 0.001$) differed significantly between land-use types. Except for beetle families classified as herbivores & detritivores combination (Fig 6F), the natural forest had significantly

higher activity densities for all trophic groups. The gravel site recorded the lowest activity density for all trophic groups (Fig. 6).

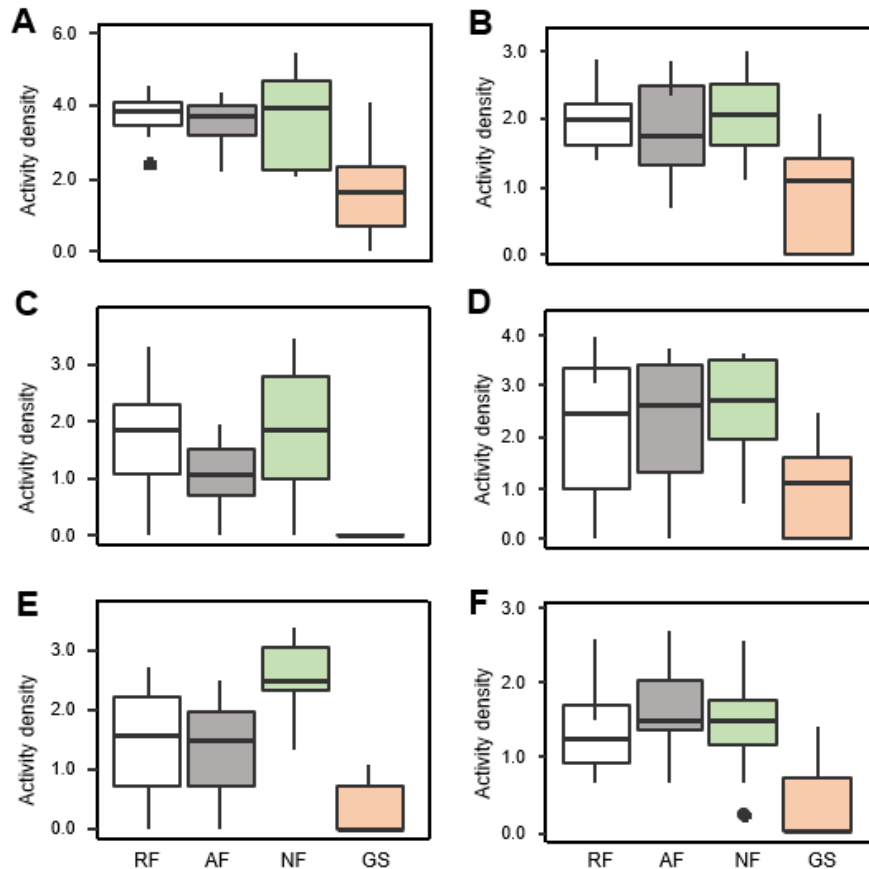


Figure 6 Box plots for activity densities in different trophic groups of beetle functional groups (A, detritivores; B, herbivores; C, fungivores, D, carnivores; E, carnivores & detritivores, and F, herbivores & detritivores) between land-use types: RF, restored forest; AF, agroforestry plantation; NF, natural forest and GS, gravel site. Single points indicate outliers based on Median and Interquartile Deviation Method (IQD).

Discussion

Our comparison of arthropod communities between an actively restored post-mining forest, a dominant alternative land-use type (agroforestry plantation), a natural reference (natural forest) and an unmanaged former mining area (gravel

mine) provides the first assessment of the effects of land-use decisions in former mining areas in Western Africa on arthropod communities. The observed pronounced differences between communities at a relatively coarse level of taxonomic (order to family) and functional (spider hunting guilds and beetle trophic groups) classification emphasize the need to address these effects in times of global insect decline (Cardoso et al., 2020; Wagner et al., 2021).

Taxonomic composition of arthropod communities

The observed dominance structure in the studied arthropod communities supports our hypothesis that land-use types with diverse and heterogeneous vegetation structure (Tab. 1) support a greater range of arthropod taxa and overall higher activity density (see also Gardner et al., 1995; Mata et al., 2020; Dampney et al., 2022a). The land-use types dominated by trees in this study (natural forest, agroforestry plantation and restored forest) offered additional niches and resources to support the activity of arthropods compared to the unrestored gravel mine. Meloni et al. (2020) showed that even ground-dwelling arthropods benefit from more diverse vegetation and the resulting habitat attributes. Diverse vegetation provides more refuge and protection from predators, resulting in higher survival and reproductive success in potential prey taxa (Wenninger & Inouye, 2008; Zou et al., 2013). For predators, diverse vegetation often correlates with higher prey availability supplying food needs (Schuldt et al., 2011; Štokmane & Spunģis, 2016; Staab & Schuldt, 2020). Deadwood and litter further promote the activity of detritivores, fungivores and arthropod predators that are part of the detritivores food web in forests (Sereda et al., 2012, 2015; Tonin et al., 2018).

Heimonen et al. (2013) emphasised the pronounced seasonal variation of herbivorous insects (e.g., mostly Orthopteroidea) that is common in tropical rain forests. For example, increasing resource concentration in the wet season is a significant factor in determining the population size in specialist herbivore populations (Doublet et al., 2019) and beetle communities (deCastro-Arazola et al., 2018). The observed differences between the two seasons support our

hypothesis that arthropod taxonomic composition is strongly influenced by seasonality across the different land-use types in our study (Lingbeek et al., 2017). Richards & Windsor (2007) observed significant seasonal variation in arthropod abundance in a lowland moist forest. Similarly, Wagner (2001) observed significant seasonal changes in arthropod fauna in a rain forest. Our study observed a higher activity density of Orthoptera (mainly herbivorous) and Polydesmida (mainly detritivorous) in the wet season than in the dry season. Several factors related to macro and micro-climatic changes (e.g., temperature, rainfall, humidity, day length, decomposition rate of organic materials etc.) might have caused this pattern (Halsch et al., 2021; Wardhaugh et al., 2018; Belchior et al., 2016; Anu et al., 2009). In addition to abiotic conditions, food resources fluctuate seasonally, further affecting arthropod emergence, activity, and reproduction (Silva et al., 2011; Richards & Windsor, 2007). Therefore, both structure- and resource-mediated effects likely affected arthropod communities between the seasons (Diehl et al. 2012). Independent of season, arthropod communities changed along a management intensity gradient in the sequence of agroforestry plantations to actively restore to natural forest arthropod communities. Therefore, the restored communities hold an intermediate position between the plantations and natural forests.

Spider families and hunting guilds

Similar to arthropod communities in general, spider communities are affected by vegetation structure, the presence of potential prey, as well as changes in abiotic conditions (Yamazaki et al., 2017; Rosa et al., 2018; Müller et al., 2022). The restored and natural forests were taxonomically richer than the agroforestry plantation and the gravel site, reflecting the various ecological niches that forest ecosystems provide to arthropods (Rosa et al., 2018). Generally, more complex vegetation offers a wider range of prey (e.g., (Diehl et al., 2013) as well as more diverse niches for spiders (Cardoso et al., 2011; Stańska et al., 2018). The observed higher activity-density of spiders in the wet season results from

precipitation, which drives plant growth as food for insects acting as prey for spiders (Rodríguez-Rodríguez et al., 2015). Spiders that construct sensing webs had higher activity-densities in the land-use types dominated by trees resulting from the higher vegetation density and availability of web sites (see Pinto et al., 2021). Balfour & Rypstra (1998) emphasised the role of habitat structure for web support and the availability of suitable microhabitats for web-building spiders. Ambush hunters also had a higher activity-density in land-use types that were dominated by trees. Ambush hunters (e.g., Thomisidae) often hide in flowers or on leaves to catch prey (Heiling et al., 2006; Willemart & Lacava, 2017) and, therefore, also rely on vegetation structure.

Beetle families and trophic groups

The activity-density of beetles even differed between the three land-use types with trees, with the restored forest (dominated by non-native tree species, e.g., *Tectona grandis*, *Senna siamiae*) recording lower activity-densities than the agroforestry plantation and the natural forest. This trend is in line with previous studies that observed a lower beetle diversity in a non-native forest plantation, such as a restored forest, compared to an old-native forest (Fischer & Lindenmayer, 2007). This pattern could be attributed to the fact that younger restored forests still support fewer tree species with limited ability to offer food and niches compared to forests of intermediate age (Lachat et al., 2012).

Moreover, the lower activity-density of beetles in the open gravel site could be attributed to the absence or limited availability of suitable habitats and food resources (Perry et al., 2016). The family Cetoniidae associated with the land-use types with trees has feeding preferences for plant tissues, exudates, and organic materials (deadwood) (Mudge et al., 2012), which characterised the forest plots in this study. The higher activity-density of Cetoniidae in the tree land-use types could be due to the potential existence of numerous ant colonies (not quantified in this study) for which several species of Cetonidae are predators (Holm & Marais, 1992). Expectedly, most beetle families showed higher activity-density in the wet

than in the dry season, in line with previous studies documenting higher diversities of beetles compared to the dry season (Andresen, 1999; Nyeko, 2009) and often attributed to the higher quality and quantity of food resources in the wet season (Wardhaugh et al., 2018).

Similar to the activity-density of arthropods, all trophic groups of beetles classified in this study showed significantly higher activity-density in the "tree" land-use types than in the "open" gravel site affirming the positive relationship between beetle functional groups and high vegetation structure (Sattler et al., 2010; Dampney et al., 2022a). Trophic groups such as detritivores (Wende et al., 2017; Mestre et al., 2018; Parisi et al., 2018) or herbivores (O'Brien et al., 2017) may have benefited from resources and habitat conditions provided by deadwood and leaf litter in the land-use types with trees. Similar to spiders, predaceous beetles may have also benefited from the higher prey availability in these land-use types (Diehl et al., 2013; Dampney et al., 2021).

Conclusion

The studied active forest restoration shows some promise in moving arthropod communities towards states observed in the natural forest, but arthropod communities in the agroforestry plantations were already more dissimilar. The patterns in arthropod communities observed for the land-use types depended on seasons, with the wet season making essential resources available for arthropods. Leaving former mining sites unmanaged is not a promising option, as arthropod communities and their habitat resource requirements were poor in the gravel site compared to the restored and natural reference forest and even the agroforestry plantation. We recommend that restoration activities in degraded post-mining regions of Ghana should focus on using mostly native tree species since they have the ability to supply habitat and food resources tailored to the needs of local biodiversity.

Data availability statement

The data that support the findings of this study are openly available in figshare <https://doi.org/10.6084/m9.figshare.16556211.v1>

Authors contributions: All authors contributed to the study's conception and design. Material preparation, data collection and analysis were performed by FGD, ED, and KB. FGD wrote the first draft of the manuscript and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Conflicts of Interest: On behalf of all authors, the corresponding author states no conflict of interest.

Acknowledgement

We are grateful to Newmont Gold Ghana Limited, the Forest Service Division of Ghana and the Terchire community for making the study sites available. We declare that no financial support was received from Newmont Gold Ghana Limited or the Forest Service Division of Ghana. We would like to thank the reviewers and the editor for their comments on a previous version, and we appreciate the contributions of Daniel Kwame Debrah and Pascal Agro Prince during the fieldwork. Kwadwo Gyasi Asante, Lanya Feng, Benjamin Schnerch, Sarina Böttner, Julia Yeboah, Tarek Hossain Raju and Christos Konstantinos Paxinos helped with sorting the arthropods into various taxonomic groups. We also appreciate the logistical support and guidance of Dr. Danilo Harms. The scholarship support from the Catholic Academic Exchange Service (KAAD) to FGD is greatly appreciated.

Appendix

Table A1 Number of individual arthropod order/suborder for land-use types (RF, restored forest; AF, agroforestry plantation; NF, natural forest and GS, gravel site) and seasons (DS, dry; WS, wet)

Order/suborder	Land-use types				Seasons	
	RF	AF	NF	GS	DS	WS
Acari	83	27	176	0	102	184
Araneae	984	567	1064	477	1173	1919
Blattodea	366	208	1276	0	784	1066
Coleoptera	1330	1555	2656	223	1400	4364
Glomerida	701	123	682	14	421	1099
Hemiptera	189	195	359	109	616	236
Hymenoptera	7098	4471	7979	2042	8716	12874
Julida	261	336	409	0	453	553
Opiliones	13	6	21	0	0	40
Orthoptera	2299	1629	1502	1709	3103	4036
Polydesmida	69	90	35	7	0	201
Ricinulei	5	2	4	0	0	11
Scolopendra	1	0	1	0	0	2
Scorpiones	4	2	5	0	0	11
Total	13403	9211	16169	4581	16768	26596

References

- Anderson M (2005) Distance-Based Tests for Homogeneity of Multivariate Dispersions. *Biometrics* 62: 245-253. doi:10.1111/j.1541-0420.2005.00440.x.
- Andresen E (1999) Seed Dispersal by Monkeys and the Fate of Dispersed Seeds in a Peruvian Rain Forest. *Biotropica* 31: 145. doi:10.2307/2663968.
- Asare D, Ansong M, Kyereh B, Dampney FG, Asante W (2022) Mining methods exert differential effects on species recruitment at artisanal small-scale mining sites in Ghana. *Heliyon* 8: e09434. doi: 10.1016/j.heliyon. 2022 e09434.
- Balfour RA, Rypstra AL (1998) The influence of habitat structure on spider density in a no-till soybean agroecosystem. *Journal of Arachnology*, 26: 221-226.
- Basset Y, Cizek L, Cuénoud P, Didham R, Novotny V, Ødegaard F, Roslin T, Tishechkin A, Schmidl J, Winchester N, Roubik D, Aberlenc H, Bail J, Barrios H, Bridle J, Castaño-Meneses G, Corbara B, Curletti G, Duarte da

- Rocha W, De Bakker D, Delabie J, Dejean A, Fagan L, Floren A, Kitching R, Medianero E, Gama de Oliveira E, Orivel J, Pollet M, Rapp M, Ribeiro S, Roisin Y, Schmidt J, Sørensen L, Lewinsohn T, Leponce M (2015) Arthropod Distribution in a Tropical Rainforest: Tackling a Four Dimensional Puzzle. PLOS ONE 10: e0144110. doi: 10.1371/journal.pone.0144110.
- Biondi M, Urbani F, D'Alessandro P (2015) Relationships between the geographic distribution of phytophagous insects and different types of vegetation: A case study of the flea beetle genus *Chaetocnema* (Coleoptera: Chrysomelidae) in the Afrotropical region. European Journal of Entomology 112: 311-327. doi:10.14411/eje.2015.040.
- Birkhofer K, Andersson G, Bengtsson J, Bommarco R, Dänhardt J, Ekbohm B, Ekroos J, Hahn T, Hedlund K, Jönsson A, Lindborg R, Olsson O, Rader R, Rusch A, Stjernman M, Williams A, Smith H (2018) Relationships between multiple biodiversity components and ecosystem services along a landscape complexity gradient. Biological Conservation 218: 247-253. doi: 10.1016/j.biocon.2017.12.027.
- Birkhofer K, Smith H, Weisser W, Wolters V, Gossner M (2015) Land-use effects on the functional distinctness of arthropod communities. Ecography 38: 889-900. doi:10.1111/ecog.01141.
- Cardoso P, Barton P, Birkhofer K, Chichorro F, Deacon C, Fartmann T, Fukushima C, Gaigher R, Habel J, Hallmann C, Hill M, Hochkirch A, Kwak M, Mammola S, Ari Noriega J, Orfinger A, Pedraza F, Pryke J, Roque F, Settele J, Simaika J, Stork N, Suhling F, Vorster C, Samways M (2020) Scientists' warning to humanity on insect extinctions. Biological Conservation 242: 108426. doi: 10.1016/j.biocon.2020.108426.
- Cardoso P, Pekár S, Jocqué R, Coddington J (2011) Global Patterns of Guild Composition and Functional Diversity of Spiders. PLoS ONE 6: e21710. doi: 10.1371/journal.pone.0021710.
- Clarke KR, Gorley RN (2015) Getting started with PRIMER v7. PRIMER-E: Plymouth: Plymouth Marine Laboratory

- Clarke KR, Gorley RN, Somerfield PJ, Warwick RM (2014) *Change in marine communities: an approach to statistical analysis and interpretation*. 3rd edition. PRIMER-E Ltd.: Plymouth
- Culliney T (2013) Role of Arthropods in Maintaining Soil Fertility. *Agriculture* 3: 629-659. doi:10.3390/agriculture3040629.
- Dampney FG, Birkhofer K, Nsiah P, de la Riva E (2020) Soil Properties and Biomass Attributes in a Former Gravel Mine Area after Two Decades of Forest Restoration. *Land* 9: 209. doi:10.3390/land9060209.
- Dampney FG, Frimpong B, Debrah D, Agro P, Wiafe E (2022a) Vegetation attributes drive the taxonomic richness and functional composition of beetles and spiders in mountainous urban green spaces. *Energy, Ecology and Environment* 7: 268-280. doi:10.1007/s40974-021-00236-z.
- Dampney FG, Birkhofer K, Oliveras Menor I, de la Riva E (2022b) The Functional Structure of Tropical Plant Communities and Soil Properties Enhance Ecosystem Functioning and Multifunctionality in Different Ecosystems in Ghana. *Forests* 13: 297. doi:10.3390/f13020297.
- Dampney FG, de la Riva E, Birkhofer K (2021) 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. *Frontiers in Forests and Global Change* 4. doi:10.3389/ffgc.2021.630959.
- Dangles O, Casas J (2019) Ecosystem services provided by insects for achieving sustainable development goals. *Ecosystem Services* 35: 109-115. doi:10.1016/j.ecoser.2018.12.002.
- deCastro-Arazola I, Hortal J, Moretti M, Sánchez-Piñero F (2018) Spatial and temporal variations of aridity shape dung beetle assemblages towards the Sahara Desert. *PeerJ* 6: e5210. doi:10.7717/peerj.5210.
- Diehl E, Sereda E, Wolters V, Birkhofer K (2013) Effects of predator specialisation, host plant and climate on biological control of aphids by natural enemies: a meta-analysis. *Journal of Applied Ecology* 50: 262-270. doi:10.1111/1365-2664.12032.

- Dippenaar-Schoeman AS, Jocqué R (1997) African spiders: an identification manual. Plant Protection Research Institute. Handbook No. 9. Agricultural Research Council of South Africa, Pretoria. iv + 392 pp.
- Doublet V, Gidoïn C, Lefèvre F, Boivin T (2019) Spatial and temporal patterns of a pulsed resource dynamically drive the distribution of specialist herbivores. *Scientific Reports* 9. doi:10.1038/s41598-019-54297-6.
- Fischer J, & Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Global ecology and biogeography*, 16(3), 265-280. doi.org/10.1111/j.1466-8238.2007.00287.x
- Gagnarli E, Valboa G, Vignozzi N, Goggioli D, Guidi S, Tarchi F, Corino L, Simoni S (2021) Effects of Land-Use Change on Soil Functionality and Biodiversity: Toward Sustainable Planning of New Vineyards. *Land* 10: 358. doi:10.3390/land10040358.
- Gardner S, Cabido M, Valladares G, Diaz S (1995) The influence of habitat structure on arthropod diversity in Argentine semi-arid Chaco forest. *Journal of Vegetation Science* 6: 349-356. doi:10.2307/3236234.
- Greenslade, P. J. M. (1964). Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *The Journal of Animal Ecology*, 301-310.
- Heiling AM, Cheng K, Herberstein ME (2006) Picking the right spot: crab spiders position themselves on flowers to maximise prey attraction. *Behaviour* 143: 957-968. doi:10.1163/156853906778623662.
- Heimonen K, Lwanga JS, Mutanen M, Nyman T, Roininen H (2013) Spatial and temporal variation in community composition of herbivorous insects on *Neoboutonia macrocalyx* in a primary tropical rain forest. *Journal of Tropical Ecology*, 29; 229-241. doi:[10.1017/S0266467413000151](https://doi.org/10.1017/S0266467413000151)
- Holm E, Marais, E (1992) *Fruit Chafers of Southern Africa (Scarabaeidae: Cetoniini)*; Ekogilde: Hartbeespoort, South Africa, 1–326.
- Høye T, Culler L (2018) Tundra arthropods provide key insights into ecological responses to environmental change. *Polar Biology* 41: 1523-1529. doi:10.1007/s00300-018-2370-x.

- Huberty A, Denno R (2004) Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* 85: 1383-1398. doi:10.1890/03-0352.
- Isaacs R, Tuell J, Fiedler A, Gardiner M, Landis D (2009) Maximising arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* 7: 196-203. doi:10.1890/080035.
- Lachat T, Wermelinger B, Gossner M, Bussler H, Isacsson G, Müller J (2012) Saproxylic beetles as indicator species for deadwood amount and temperature in European beech forests. *Ecological Indicators* 23: 323-331. doi: 10.1016/j.ecolind.2012.04.013.
- Lassau SA, Hochuli D, Cassis G, Reid C (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Diversity and Distributions* 11: 73-82. doi:10.1111/j.1366-9516.2005.00124.x. <https://doi.org/10.1111/j.1366-9516.2005.00124.x>
- Lingbeek BJ, Higgins C, Muir J, Kattes D, Schwertner T (2017) Arthropod diversity and assemblage structure response to deforestation and desertification in the Sahel of western Senegal. *Global Ecology and Conservation* 11: 165-176. doi: 10.1016/j.gecco.2017.06.004.
- Mata L, Andersen A, Morán-Ordóñez A, Hahs A, Backstrom A, Ives C, Bickel D, Duncan D, Palma E, Thomas F, Cranney K, Walker K, Shears I, Semeraro L, Malipatil M, Moir M, Plein M, Porch N, Vesik P, Smith T, Lynch Y (2021) Indigenous plants promote insect biodiversity in urban greenspaces. *Ecological Applications*. doi:10.1002/eap.2309.
- May R (2010) Tropical Arthropod Species, More or Less? *Science* 329: 41-42. doi:10.1126/science.1191058.
- Meloni F, Civieta B, Zaragoza J, Lourdes Moraza M, Bautista S (2020) Vegetation Pattern Modulates Ground Arthropod Diversity in Semi-Arid Mediterranean Steppes. *Insects* 11: 59. doi:10.3390/insects11010059.
- Mestre L, Jansson N, Ranius T (2018) Saproxylic biodiversity and decomposition

- rate decrease with small-scale isolation of tree hollows. *Biological Conservation* 227: 226-232. doi: 10.1016/j.biocon.2018.09.023.
- Millard J, Outhwaite C, Kinnersley R, Freeman R, Gregory R, Adedjoja O, Gavini S, Kioko E, Kuhlmann M, Ollerton J, Ren Z, Newbold T (2021) Global effects of land-use intensity on local pollinator biodiversity. *Nature Communications* 12. doi:10.1038/s41467-021-23228-3.
- Mudge AD, Orozco J, Keith Philips T, Antoine P (2012) The cetoniine fauna of the Upper Guinean forests and savannas of Ghana (Coleoptera: Scarabaeidae: Cetoniinae). *Terrestrial Arthropod Reviews* 5: 113-174. doi:10.1163/187498312x635319.
- Müller J, Brandl R, Cadotte M, Heibl C, Bässler C, Weiß I, Birkhofer K, Thorn S, Seibold S (2022) A replicated study on the response of spider assemblages to regional and local processes. *Ecological Monographs*. doi:10.1002/ecm.1511.
- Newbold T (2018) Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society B: Biological Sciences* 285: 20180792. doi:10.1098/rspb.2018.0792.
- Novotny V, Basset Y, Miller S, Weiblen G, Bremer B, Cizek L, Drozd P (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature* 416: 841-844. doi:10.1038/416841a.
- Nyeko P (2009) Dung Beetle Assemblages and Seasonality in Primary Forest and Forest Fragments on Agricultural Landscapes in Budongo, Uganda. *Biotropica* 41: 476-484. doi:10.1111/j.1744-7429.2009.00499.x.
- Nyffeler M, Olson E, Symondson W (2016) Plant-eating by spiders. *Journal of Arachnology* 44: 15-27. doi:10.1636/p15-45.1.
- O'Brien M, Brezzi M, Schuldt A, Zhang J, Ma K, Schmid B, Niklaus P (2017) Tree diversity drives diversity of arthropod herbivores, but successional stage mediates detritivores. *Ecology and Evolution* 7: 8753-8760. doi:10.1002/ece3.3411.

- Ødegaard F (2000) How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society* 71: 583-597. doi:10.1111/j.1095-8312.2000.tb01279. x.
- Ofosu G, Dittmann A, Sarpong D, Botchie D (2020) Socio-economic and environmental implications of Artisanal and Small-scale Mining (ASM) on agriculture and livelihoods. *Environmental Science & Policy* 106: 210-220. doi: 10.1016/j.envsci.2020.02.005.
- Ontl T, Janowiak M, Swanston C, Daley J, Handler S, Cornett M, Hagenbuch S, Handrick C, Mccarthy L, Patch N (2020) Forest Management for Carbon Sequestration and Climate Adaptation. *Journal of Forestry* 118: 86-101. doi:10.1093/jofore/fvz062.
- Owusu K, Waylen P (2012) The changing rainy season climatology of mid-Ghana. *Theoretical and Applied Climatology* 112: 419-430. doi:10.1007/s00704-012-0736-5.
- Parisi F, Pioli S, Lombardi F, Fravolini G, Marchetti M, Tognetti R (2018) Linking deadwood traits with saproxylic invertebrates and fungi in European forests - a review. *iForest - Biogeosciences and Forestry* 11: 423-436. doi:10.3832/ifor2670-011.
- Perner J, Schueler S (2004) Estimating the density of ground-dwelling arthropods with pitfall traps using a nested-cross array. *Journal of Animal Ecology* 73: 469-477. doi:10.1111/j.0021-8790.2004.00821. x.
- Perry J, Lojka B, Quinones Ruiz L, Van Damme P, Houška J, Fernandez Cusimamani E (2016) How natural Forest Conversion Affects Insect Biodiversity in the Peruvian Amazon: Can Agroforestry Help? *Forests* 7: 82. doi:10.3390/f7040082.
- Picanço A, Rigal F, Matthews T, Cardoso P, Borges P (2017) Impact of land-use change on flower-visiting insect communities on an oceanic island. *Insect Conservation and Diversity* 10: 211-223. doi:10.1111/icad.12216.
- Picker M (2012) *Field guide to insects of South Africa*. Penguin Random House, South Africa

- Pinto C, Pairo P, Bellocq M, Filloy J (2021) Different land-use types equally impoverish but differentially preserve grassland species and functional traits of spider assemblages. *Scientific Reports* 11. doi:10.1038/s41598-021-89658-7.
- R Core Team (2019) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. [https://doi.org/ISBN 3-900051-07-0](https://doi.org/ISBN%203-900051-07-0).
- Rader R, Bartomeus I, Garibaldi L, Garratt M, Howlett B, Winfree R, Cunningham S, Mayfield M, Arthur A, Andersson G, Bommarco R, Brittain C, Carnevali L, Chacoff N, Entling M, Foully B, Freitas B, Gemmill-Herren B, Ghazoul J, Griffin S, Gross C, Herbertsson L, Herzog F, Hipólito J, Jaggard S, Jauker F, Klein A, Kleijn D, Krishnan S, Lemos C, Lindström S, Mandelik Y, Monteiro V, Nelson W, Nilsson L, Pattenmore D, de O. Pereira N, Pisanty G, Potts S, Reemer M, Rundlöf M, Sheffield C, Scheper J, Schüepp C, Smith H, Stanley D, Stout J, Szentgyörgyi H, Taki H, Vergara C, Viana B, Woyciechowski M (2016) Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences* 113: 146-151. doi:10.1073/pnas.1517092112.
- Richards L, Windsor D (2007) Seasonal variation of arthropod abundance in gaps and the understorey of a lowland moist forest in Panama. *Journal of Tropical Ecology* 23: 169-176. doi:10.1017/s0266467406003907.
- Rodríguez-Rodríguez S, Solís-Catalán K, Valdez-Mondragón A (2015) Diversity and seasonal abundance of anthropogenic spiders (Arachnida: Araneae) in different urban zones of the city of Chilpancingo, Guerrero, Mexico. *Revista Mexicana de Biodiversidad* 86: 962-971. doi: 10.1016/j.rmb.2015.09.002.
- Rosa M, Santos J, Brescovit A, Mafra Á, Baretta D (2018) Spiders (Arachnida: Araneae) in Agricultural Land Use Systems in Subtropical Environments. *Revista Brasileira de Ciência do Solo* 42. doi:10.1590/18069657rbc20160576.
- Sagi N, Hawlena D (2021) Arthropods as the Engine of Nutrient Cycling in Arid Ecosystems. *Insects* 12: 726. doi:10.3390/insects 12080726.

- Sattler T, Duelli P, Obrist M, Arlettaz R, Moretti M (2010) Response of arthropod species richness and functional groups to urban habitat structure and management. *Landscape Ecology* 25: 941-954. doi:10.1007/s10980-010-9473-2.
- Schowalter T (2017) Arthropod Diversity and Functional Importance in Old-Growth Forests of North America. *Forests* 8: 97. doi:10.3390/f8040097.
- Schroeder H, Grab H, Kessler A, Poveda K (2021) Human-Mediated Land Use Change Drives Intraspecific Plant Trait Variation. *Frontiers in Plant Science* 11. doi:10.3389/fpls.2020.592881.
- Schueler V, Kuemmerle T, Schröder H (2011) Impacts of Surface Gold Mining on Land Use Systems in Western Ghana. *AMBIO* 40: 528-539. doi:10.1007/s13280-011-0141-9.
- Schuldt A, Both S, Bruelheide H, Härdtle W, Schmid B, Zhou H, Assmann T (2011) Predator Diversity and Abundance Provide Little Support for the Enemies Hypothesis in Forests of High Tree Diversity. *PLoS ONE* 6: e22905. doi:10.1371/journal.pone.0022905.
- Seibold S, Gossner M, Simons N, Blüthgen N, Müller J, Ambarlı D, Ammer C, Bausch J, Fischer M, Habel J, Linsenmair K, Nauss T, Penone C, Prati D, Schall P, Schulze E, Vogt J, Wöllauer S, Weisser W (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574: 671-674. doi:10.1038/s41586-019-1684-3.
- Sereda E, Blick T, Dorow W, Wolters V, Birkhofer K (2012) Spatial distribution of spiders and epedaphic Collembola in an environmentally heterogeneous forest floor habitat. *Pedobiologia* 55: 241-245. doi:10.1016/j.pedobi.2012.03.007.
- Sereda E, Wolters V, Birkhofer K (2015) Addition of crop residues affects a detritus-based food chain depending on litter type and farming system. *Basic and Applied Ecology* 16: 746-754. doi: 10.1016/j.baae.2015.07.005.
- Silva N, Frizzas M, Oliveira C (2011) Seasonality in insect abundance in the "Cerrado" of Goiás State, Brazil. *Revista Brasileira de Entomologia* 55: 79-

87. doi:10.1590/s0085-56262011000100013.

- Somerfield P, Clarke K (2013) Inverse analysis in non-parametric multivariate analyses: distinguishing groups of associated species which covary coherently across samples. *Journal of Experimental Marine Biology and Ecology* 449: 261-273. doi: 10.1016/j.jembe.2013.10.002.
- Sonter L, Ali S, Watson J (2018) Mining and biodiversity: key issues and research needs in conservation science. *Proceedings of the Royal Society B: Biological Sciences* 285: 20181926. doi:10.1098/rspb.2018.1926.
- Staab M, Schuldt A (2020) The Influence of Tree Diversity on Natural Enemies— a Review of the "Enemies" Hypothesis in Forests. *Current Forestry Reports* 6: 243-259. doi:10.1007/s40725-020-00123-6.
- Stańska M, Stański T, Wielgosz E, Hajdamowicz I (2018) Impact of Habitat Complexity on Body Size of Two Spider Species, *Alopecosa cuneata* and *A. pulverulenta* (Araneae, Lycosidae), in River Valley Grasslands. *Polish Journal of Environmental Studies* 27: 853-859. doi:10.15244/pjoes/75806.
- Štokmane M, Spuņģis V (2016) The influence of vegetation structure on spider species richness, diversity and community organisation in the Apšuciems calcareous fen, Latvia. *Animal Biodiversity and Conservation* 39: 221-236. doi:10.32800/abc.2016.39.0221.
- Stork N (2018) How Many Species of Insects and Other Terrestrial Arthropods Are There on Earth? *Annual Review of Entomology* 63: 31-45. doi:10.1146/annurev-ento-020117-043348.
- Stuart SN, Adams RJ, Jenkins M (1990) *Biodiversity in sub-Saharan Africa and its islands: conservation, management, and sustainable use*. Occasional Paper of the IUCN Species Survival Commission, 6: 1-242.
- Tonin A, Pozo J, Monroy S, Basaguren A, Pérez J, Gonçalves J, Pearson R, Cardinale B, Boyero L (2018) Interactions between large and small detritivores influence how biodiversity impacts litter decomposition. *Journal of Animal Ecology* 87: 1465-1474. doi:10.1111/1365-2656.12876.
- Underwood E, Quinn J (2010) Response of ants and spiders to prescribed fire in

- oak woodlands of California. *Journal of Insect Conservation* 14: 359-366. doi:10.1007/s10841-010-9265-7.
- van der Sluijs J, Vaage N (2016) Pollinators and Global Food Security: the Need for Holistic Global Stewardship. *Food Ethics* 1: 75-91. doi:10.1007/s41055-016-0003-z.
- Wagner D, Grames E, Forister M, Berenbaum M, Stopak D (2021) Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences* 118. doi:10.1073/pnas.2023989118.
- Wagner T (2001) Seasonal changes in the canopy arthropod fauna in *Rinorea beniensis* in Budongo Forest, Uganda. *Tropical Forest Canopies: Ecology and Management*: 169-178. doi:10.1007/978-94-017-3606-0_13.
- Wardhaugh C, Stone M, Stork N (2018) Seasonal variation in a diverse beetle assemblage along two elevational gradients in the Australian Wet Tropics. *Scientific Reports* 8. doi:10.1038/s41598-018-26216-8.
- Wende B, Gossner M, Grass I, Arnstadt T, Hofrichter M, Floren A, Linsenmair K, Weisser W, Steffan-Dewenter I (2017) Trophic level, successional age and trait matching determine specialisation of deadwood-based interaction networks of saproxylic beetles. *Proceedings of the Royal Society B: Biological Sciences* 284: 20170198. doi:10.1098/rspb.2017.0198.
- Wenninger E, Inouye R (2008) Insect community response to plant diversity and productivity in a sagebrush–steppe ecosystem. *Journal of Arid Environments* 72: 24-33. doi: 10.1016/j.jaridenv.2007.04.005.
- Willemart RH, Lacava M (2017) Foraging strategies of cursorial and ambush spiders. in: Viera, C., Gonzaga, M.O. (Eds.), *Behaviour and ecology of spiders*. Springer International Publishing, Cham, 227–245. doi.org/10.1007/978-3-319-65717-2
- Yamazaki L, Vindica V, Brescovit A, Marques M, Battirolo L (2017) Temporal variation in the spider assemblage (Arachnida, Araneae) in canopies of *Callisthene fasciculata* (Vochysiaceae) in the Brazilian Pantanal biome. *Iheringia. Série Zoologia* 107.

doi:10.1590/1678-4766e2017019.

Zou Y, Sang W, Bai F, Axmacher J (2013) Relationships between Plant Diversity and the Abundance and α -Diversity of Predatory Ground Beetles (Coleoptera: Carabidae) in a Mature Asian Temperate Forest Ecosystem. PLoS ONE 8: e82792. doi:10.1371/journal.pone.0082792.

Chapter VI: 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

Published: 12th May 2021 in **Frontiers in Forests and Global Change 2021**, 4

[https:// doi: 10.3389/ffgc.2021.630959](https://doi.org/10.3389/ffgc.2021.630959)

Frederick Gyasi Damp^{1*}, Enrique G. de la Riva¹, Klaus Birkhofer¹

¹ Department of Ecology, Brandenburg University of Technology, 03046
Cottbus, Senftenberg, Germany

frederickGyasi.Damp¹@b-tu.de (F.G.D.)

enrique.garciadelariva@b-tu.de (E.G.d.I.R.)

klaus.birkhofer@b-tu.de (K.B.)

***Corresponding author**

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

Frederick Gyasi Damphey*, Enrique G. de la Riva, Klaus Birkhofer

Department of Ecology, Brandenburg University of Technology, 03046
Cottbus, Senftenberg, Germany

* Correspondence: FrederickGyasi.Damphey@b-tu.de

Received: 18 November 2020: Accepted: 15 April 2021: Published: 12 May 2021

Abstract

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 plantation 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 × 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 ≥ 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 plantation. 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 plantation and the restored forest. The actively restored forest took an intermediate position between the agroforestry plantation 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 plantation, but at the cost of lower food and fuelwood biomass and carbon storage compared to natural forests.

Keywords: active restoration, biodiversity, deforestation, ecosystem services, forest, Ghana, mining

1. 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; Dampney 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 aesthetic 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 analysed 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 (Dampney et al., 2020). ES proxies were assessed in the following categories: (a) food-related tree ES (biomass of food and fodder trees), (b) other tree 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 analyse 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.

2. Materials and methods

2.1. Study Area

The three forest areas are Terchire restoration area (actively “restored forest”), Bosomkese forest reserve (“agroforestry plantation”) 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 2m × 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 plantation 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) (Dampney et al., 2020).

2.2. Sampling Design

Eight plots (20 × 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 & 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 ($\frac{\text{No. of individuals of species A}}{\text{Total no. of individuals of all species}} \times 100$), frequency ($\frac{\text{Frequency of species A}}{\text{Sum of frequency values for all species}} \times 100$) and abundance ($\frac{\text{Total no. of individuals found}}{\text{No. of quadrats of occurrence}} \times 100$) 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; <http://tropical.theferns.info/>; 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 (ρ) based on an improved allometric equation for the tropical trees ($\ln(\text{AGB}) = \alpha + \beta \ln(\rho \times D^2 \times H) + \varepsilon$; Chave et al., 2014). The specific wood density for each tree was obtained from several database or sources (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 ten 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 odour-free detergent to reduce the surface tension (Schmidt et al., 2006; Pais & Varanda, 2010). Traps were then sheltered by small rain covers to minimize dilution by rain (Underwood & Quinn, 2010). Traps were left unused for one 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).

2.3. 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 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 analysed 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 analyse 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 plantation and natural forest) and 9999 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

Chapter VI: 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

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).

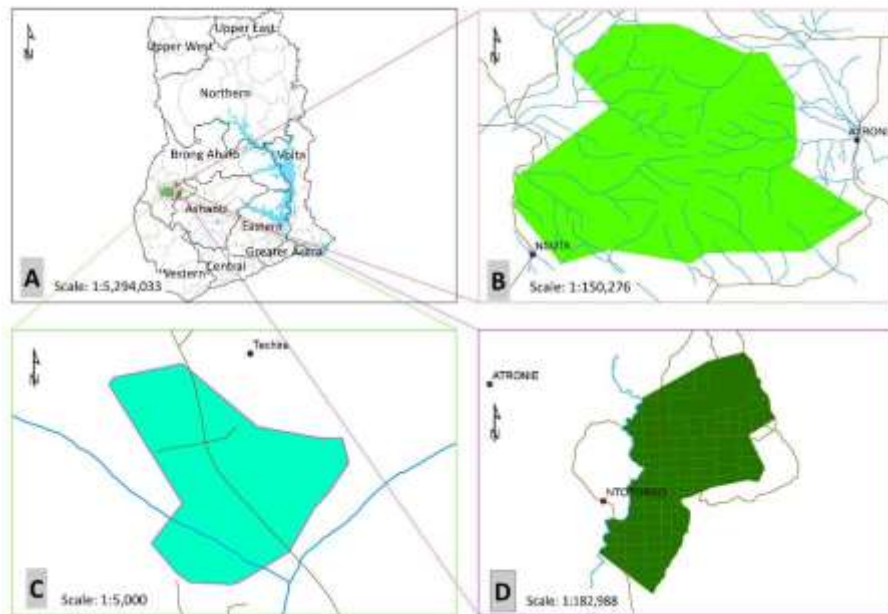


Figure 1 (A) Map of Ghana showing the (B) Natural forest (Asukese forest reserve), (C) Restored forest (Terchire restoration area) and, (D) Agroforestry plantation (Bosomkese forest reserve)

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	<i>Elaeis guineensis</i> , <i>Cola nitida</i> , <i>Dialium guineense</i> , <i>Terminalia catappa</i> , <i>Tetrapleura tetraptera</i> , <i>Artocarpus altilis</i> , <i>Mangifera indica</i>	Powell et al., 2015; Reed et al., 2017
	Fodder tree biomass	Leguminous tree parts as essential components of fodder resources for livestock	<i>Moringa oleifera</i> , <i>Leucaena leucocephala</i> , <i>Albizia ferruginea</i> , <i>Tetrapleura tetraptera</i>	Jasaw et al., 2017; Vandermeulen et al., 2018
	Medicine tree biomass	Used as traditional medicine and also raw materials for the pharmaceutical industry	<i>Tetrapleura tetraptera</i> , <i>Antidesma laciniatum</i> , <i>Moringa oleifera</i> , <i>Nesogordonia papaverifera</i>	Voeks and Rahmatian, 2004; Caballero-Serrano et al., 2019
	Fuelwood tree biomass	Supply of energy required for food production	<i>Cassia siamea</i> , <i>Celtis zenkeri</i> , <i>Leucaena leucocephala</i> , <i>Holarrhena floribunda</i>	Brockhoff et al., 2017
	Mulch-tree biomass	Leguminous tree species used to improve soil fertility	<i>Albizia zygia</i> , <i>Leucaena leucocephala</i>	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)	Brockhoff 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 & Julida)	Brockhoff et al., 2017
Cultural	Tree richness (rarefied)	Spiritual and symbolic interaction with nature	All tree species	Brockhoff et al., 2017; Kearney et al., 2019

3. Results

3.1. 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* (IVI=13.4). The agroforestry plantation was characterised 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 characterised by *Celtis mildbraedii* (IVI=34.5), *Triplochiton scleroxylon* (IVI=21.1) and *Nesogordonia papaverifera* (IVI=17.5).

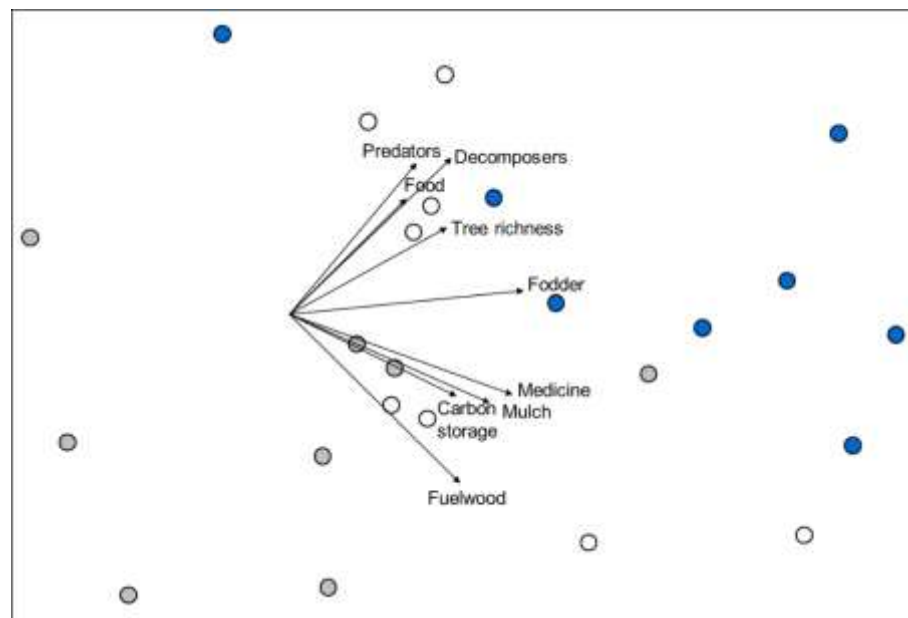


Figure 2 Non-metric multidimensional scaling ordination based on Gower similarities between plots of different forest types and values for all ES proxies (see Table 1). The 2-d stress value is 0.15. Symbol colours represent forest types: ●, agroforestry plantation (Bosomkese forest reserve); ●, natural 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.

3.2. 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 plantation 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 plantation 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 gigantea* were characteristic for the natural forest plots, while the agroforestry plantation plots were characterized by *Cola gigantea* and *Dialium guineense*.

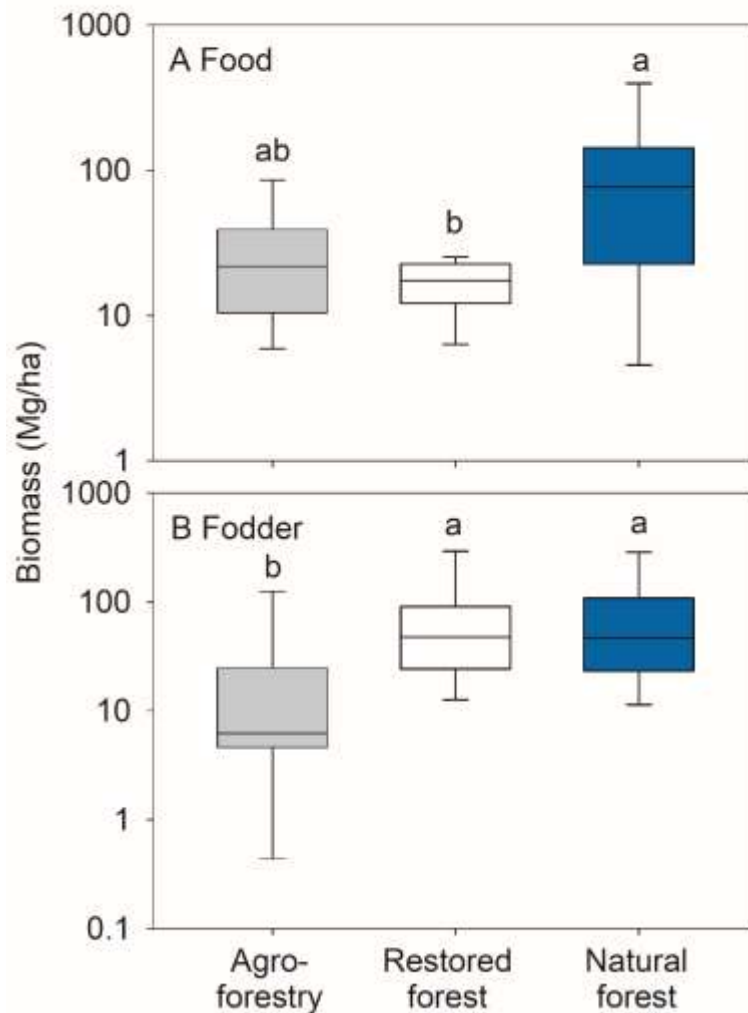


Figure 3 Box plots of A) food tree and B) fodder tree biomass in the agroforestry plantation (Bosomkese forest reserve), actively restored (Terchire restoration area) and natural forest (Asukese forest reserve; N=8 per forest type). The line represents the median value, the box limits are the 25th and 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.

3.3. 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 plantation 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 Cyrtoucheniidae and Barychelidae were more abundant in agroforestry plantation 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 plantation plots (Figure 4B). The differences between restored forest and the agroforestry plantation 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).

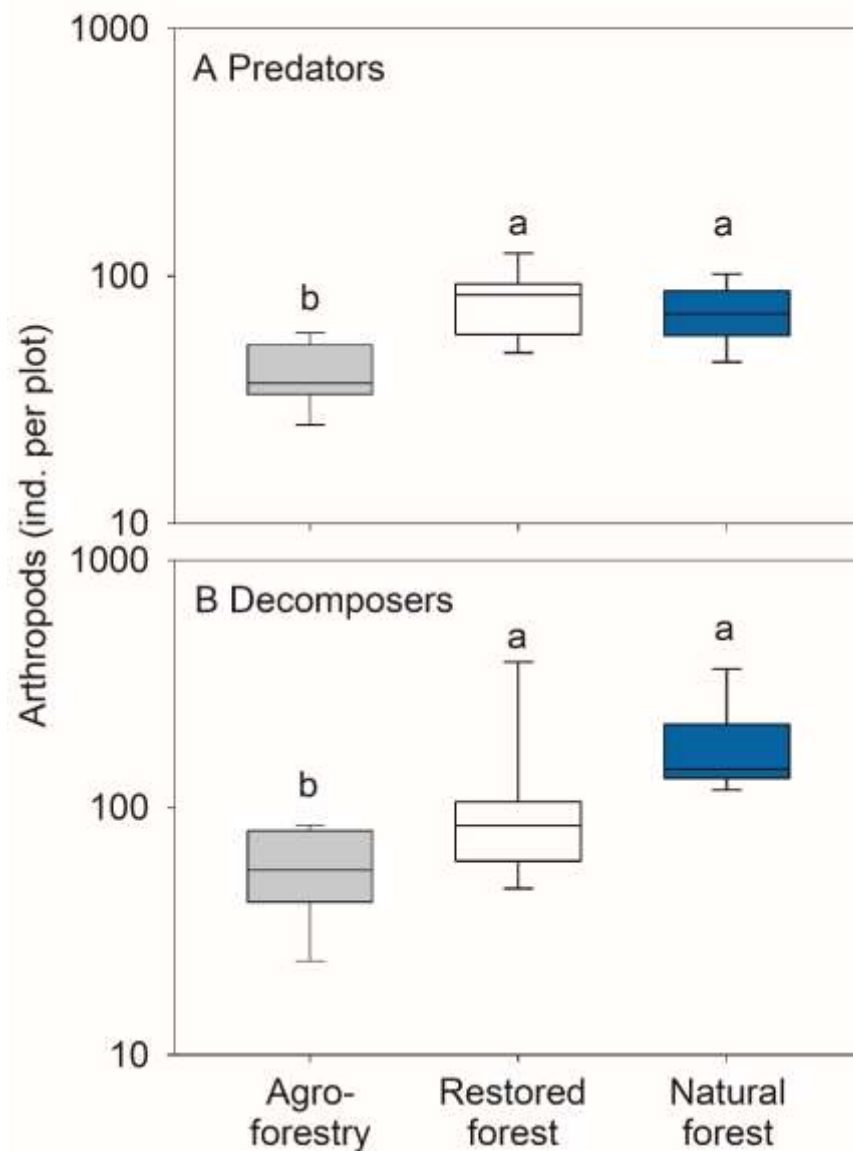


Figure 4 Box plots of arthropod A) predator and B) decomposer numbers in the agroforestry plantation (Bosomkese forest reserve), actively restored (Terchire restoration area) or natural forest (Asukese forest reserve; N=8 per forest type). The line represents the median value, the box limits are the 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 plantation ($t=2.26$; $p=0.004$) 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*.

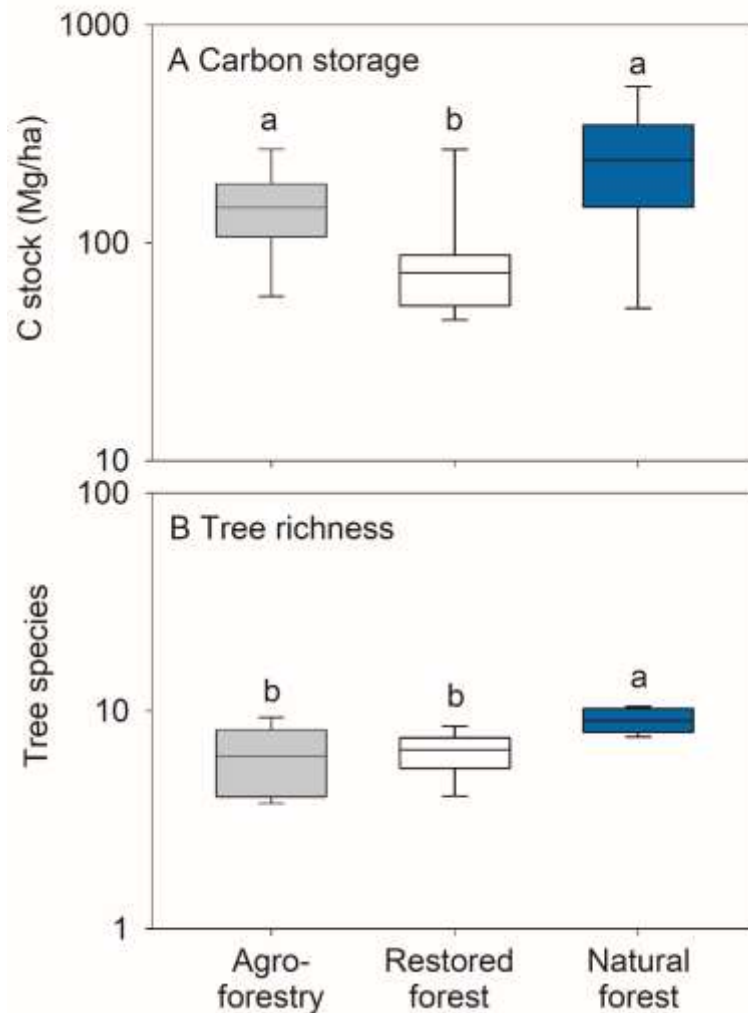


Figure 5 Box plots of A) carbon storage and B) tree species richness in the agroforestry plantation (Bosomkese forest reserve), actively restored (Terchire restoration area) or natural forest (Asukese forest reserve; N=8 per forest type). The line represents the median value, the box limits are the 25th 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.

3.4. Trade-offs and synergies in ES proxies

The natural forest had the highest relative values for all 8 out of 9 ES proxies, with carbon storage being the only exception and no apparent trade-offs between pairs of ES proxies (Figure 6).

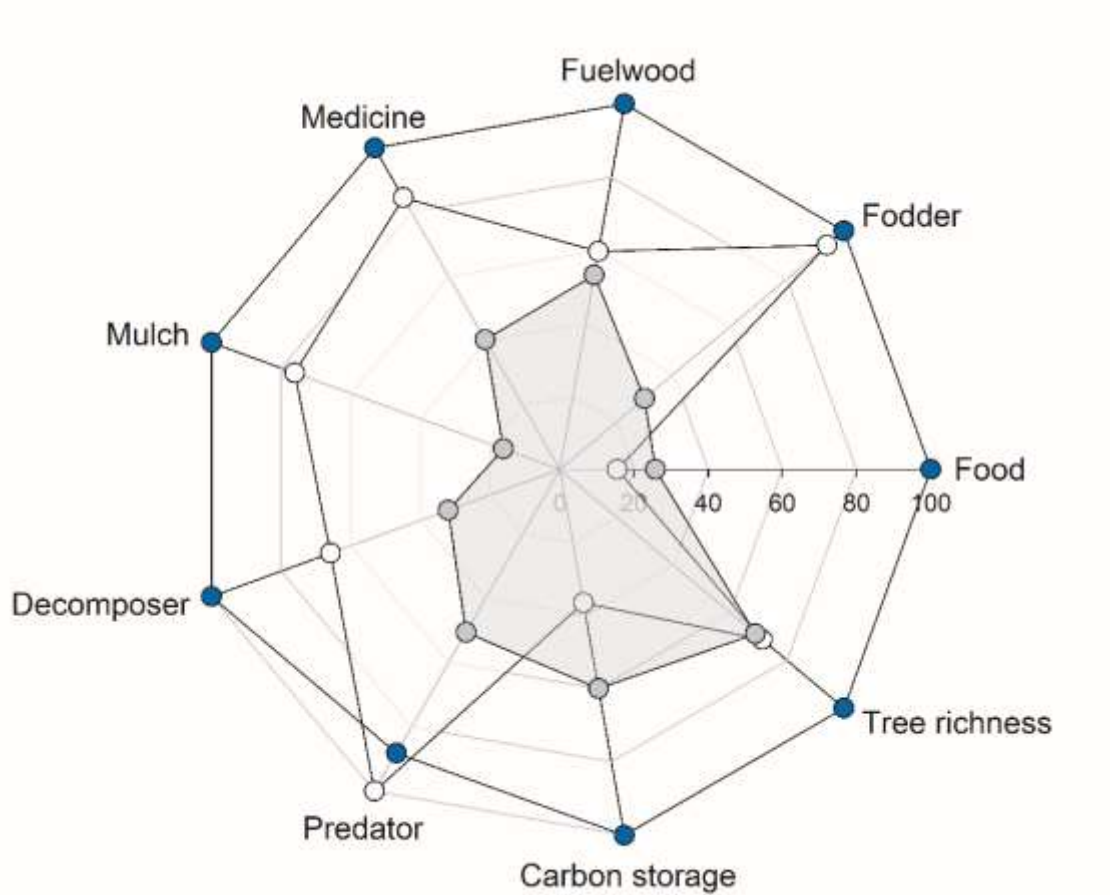


Figure 6 Rader plot showing the relationship between ecosystem service proxies in forest types: ●, agroforestry plantation (Bosomkese forest reserve); ●, natural forest (Asukese forest reserve) and ○, actively restored forest (Terchire Restoration area: N=8 per forest type). The highest average for each 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.

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).

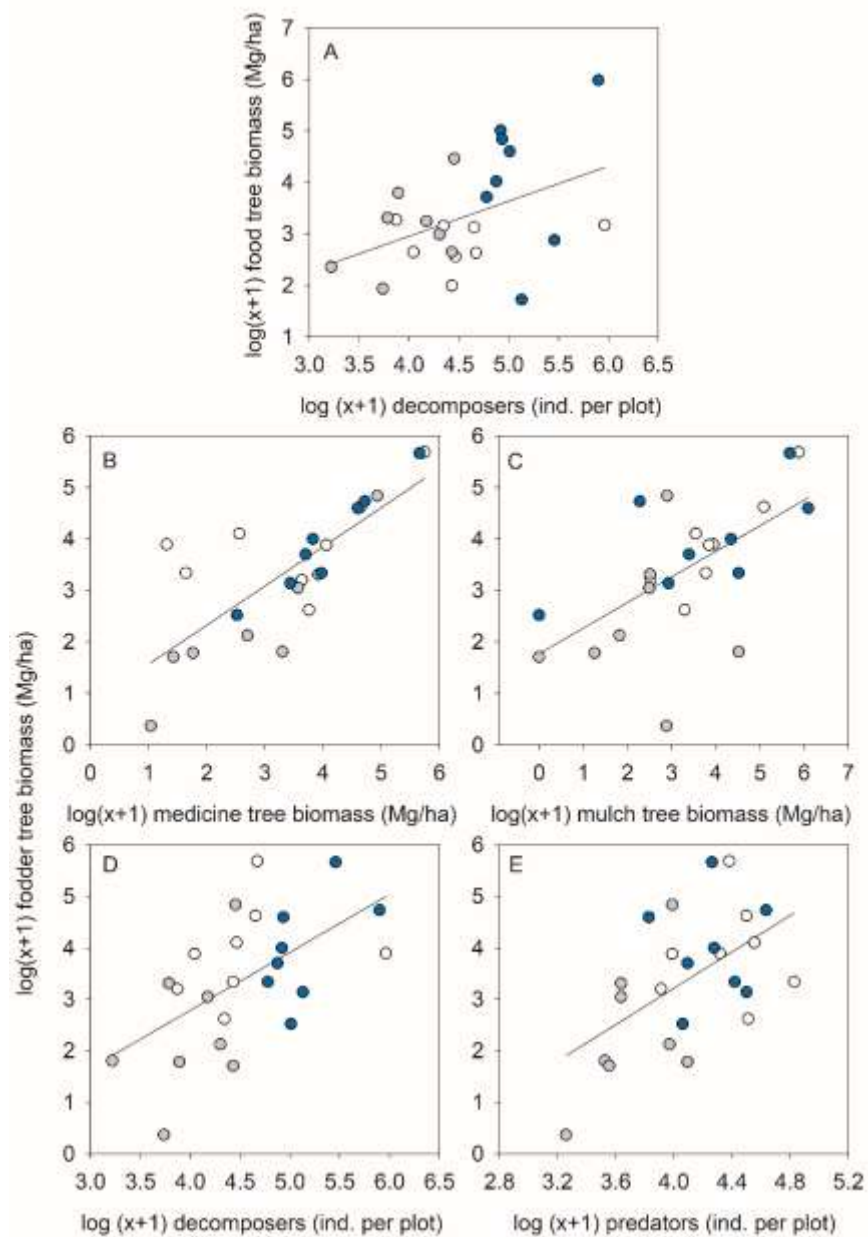


Figure 7 Relationship between A) food tree biomass and decomposer arthropod numbers, or fodder tree biomass and B) medicine tree biomass, C) mulch tree biomass, D) decomposer and E) predatory arthropod numbers across forest types: ●, agroforestry plantation (Bosomkese Forest Reserve); ●, natural forest (Asukese Forest Reserve) and ○, actively restored forest (Terchire Restoration area; N=8 per forest type).

4. Discussion

Ecosystems with diverse tree communities are often superior in the provision of multiple ecosystem services 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, carbon storage), supporting (habitat for organisms) and cultural (aesthetic, symbolic and religious) ecosystem services and determine the dynamics and functioning of forests (Blicharska & Mikusiński, 2014; Brockerhoff et al., 2017; Mori et al., 2017; Reed et al., 2017). Active restoration promoted selected ecosystem services (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.

4.1. ES proxies and forest types

Forest types offer different levels of ecosystem services 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 & 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 (Dampney et al., 2020) thereby potentially also supporting higher predator numbers.

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 ecosystem service 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 Dampney 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 towards higher levels of food tree growth if food supply is relevant for the region

4.2. 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 harbour greater predator (natural enemies) abundance which may simultaneously result in improved control of pests (Staab & Schuldt, 2020).

The fact that the majority of tree species recorded had multiple purposes to some extent 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.

5. Conclusion

Our comparison of ecosystem service 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 towards 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.

FUNDING

The scholarship support from the Catholic Academic Exchange Service (KAAD) and the Graduate Student Research Award- 2019 from the Society for Conservation Biology (SCB) to FD is greatly appreciated.

ACKNOWLEDGMENTS

We are grateful to Newmont Gold Ghana Limited and Forest Service Division of Ghana for making the study sites available. We declare that no financial support was received from Newmont Gold Ghana Limited. We would like to thank the reviewers and the editor for their comments on a previous version and we appreciate the contributions of Daniel Kwame Debrah, Frederick Nyahe, and Pascal Agro Prince for helping with the fieldwork. Special thanks to Forest Aid Ghana for providing logistical support for this research.

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>

References

- Acheampong, E. O., Macgregor, C. J., Sloan, S., & Sayer, J. (2019). Deforestation is driven by agricultural expansion in Ghana's forest reserves. *Scientific African*, 5, e00146.
- Albrich, K., Rammer, W., Thom, D., & Seidl, R. (2018). Trade-offs between temporal stability and level of forest ecosystem services provisioning under climate change. *Ecological Applications*, 28(7), 1884-1896.
- Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62(1), 245-253.
- Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). Permanova+ for Primer: Guide software and Statical methods. *Plymouth: Primer-e Available at <http://www.primer-e.com/permanova.htm>*.
- Benayas, J. M. R., & Bullock, J. M. (2012). Restoration of biodiversity and ecosystem services on agricultural land. *Ecosystems*, 15(6), 883-899.
- Bennett, E. M., Peterson, G. D., & Gordon, L. J. (2009). Understanding relationships among multiple ecosystem services. *Ecology letters*, 12(12),

1394-1404.

- Berry, Z. C., Jones, K. W., Aguilar, L. R. G., Congalton, R. G., Holwerda, F., Kolka, R., ... & Muñoz-Villers, L. (2020). Evaluating ecosystem service trade-offs along a land-use intensification gradient in central Veracruz, Mexico. *Ecosystem Services*, *45*, 101181.
- Bianchi, F. J., Booij, C. J. H., & Tschamntke, T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1595), 1715-1727.
- Birkhofer, K., Diekötter, T., Boch, S., Fischer, M., Müller, J., Socher, S., & Wolters, V. (2011). Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. *Soil Biology and Biochemistry*, *43*(10), 2200-2207.
- Birkhofer, K., Diehl, E., Andersson, J., Ekroos, J., Früh-Müller, A., Machnikowski, F., ... & Wolters, V. (2015). Ecosystem services—current challenges and opportunities for ecological research. *Frontiers in Ecology and Evolution*, *2*, 87.
- Birkhofer, K., Andersson, G. K., Bengtsson, J., Bommarco, R., Dänhardt, J., Ekbohm, B., ... & Lindborg, R. (2018). Relationships between multiple biodiversity components and ecosystem services along a landscape complexity gradient. *Biological Conservation*, *218*, 247-253.
- Birkhofer, K., Addison, P., Addison, M. F., Arvidsson, F., Bazelet, C., Bengtsson, J., ... & Kapp, C. (2019). Effects of ground cover management on biotic communities, ecosystem services and disservices in organic pome fruit orchards in South Africa. *Frontiers in Sustainable Food Systems*, *3*, 107.
- Blicharska, M., & Mikusiński, G. (2014). Incorporating social and cultural significance of large old trees in conservation policy. *Conservation Biology*, *28*(6), 1558-1567.
- Bordt, M., & Saner, M. (2019). Which ecosystems provide which services? A meta-analysis of nine selected ecosystem services assessments. *One*

Ecosystem, 4, e31420.

- Brockhoff, E. G., Barbaro, L., Castagneyrol, B., Forrester, D. I., Gardiner, B., González-Olabarria, J. R., ... & Thompson, I. D. (2017). Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity Conservation*, 26, 3005-3035.
- Bullock, J. M., Aronson, J., Newton, A. C., Pywell, R. F., & Rey-Benayas, J. M. (2011). Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends in ecology & evolution*, 26(10), 541-549.
- Caballero-Serrano, V., McLaren, B., Carrasco, J. C., Alday, J. G., Fiallos, L., Amigo, J., & Onaindia, M. (2019). Traditional ecological knowledge and medicinal plant diversity in Ecuadorian Amazon home gardens. *Global Ecology and Conservation*, 17, e00524.
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B., ... & Henry, M. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global change biology*, 20(10), 3177-3190.
- Chazdon, R. L. (2008). Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, 320(5882), 1458-1460.
- Chirwa P.W., Adeyemi O. (2019). Deforestation in Africa: Implications on Food and Nutritional Security. In: Leal Filho W., Azul A., Brandli L., Özuyar P., Wall T. (eds) Zero Hunger. Encyclopedia of the UN Sustainable Development Goals. Springer, Cham. https://doi.org/10.1007/978-3-319-69626-3_62-1
- Ciccarese, L., Mattsson, A., & Pettenella, D. (2012). Ecosystem services from forest restoration: thinking ahead. *New Forests*, 43(5-6), 543-560.
- Clarke, K. R., & Gorley, R. N. (2015). Getting started with PRIMER v7. *PRIMER-E: Plymouth, Plymouth Marine Laboratory*, 20.
- Conti, G., & Díaz, S. (2013). Plant functional diversity and carbon storage—an empirical test in semi-arid forest ecosystems. *Journal of Ecology*, 101(1), 18-28.

- Crouzeilles, R., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Sansevero, J. B., Monteiro, L., ... & Strassburg, B. B. (2017). Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances*, 3(11), e1701345.
- Curtis, J. T., & McIntosh, R. P. (1950). The interrelations of certain analytic and synthetic phytosociological characters. *Ecology*, 31(3), 434-455.
- Dampney, F. G., Birkhofer, K., Nsiah, P. K., & de la Riva, E. G. (2020). Soil Properties and Biomass Attributes in a Former Gravel Mine Area after Two Decades of Forest Restoration. *Land*, 9(6), 209.
- Dangles, O., & Casas, J. (2019). Ecosystem services provided by insects for achieving sustainable development goals. *Ecosystem services*, 35, 109-115.
- Diehl, E., Wolters, V., & Birkhofer, K. (2012). Arable weeds in organically managed wheat fields foster carabid beetles by resource-and structure-mediated effects. *Arthropod-Plant Interactions*, 6(1), 75-82.
- Donkersley, P. (2019). Trees for bees. *Agriculture, ecosystems & environment*, 270, 79-83.
- Eisenhauer, N., Vogel, A., Jensen, B., & Scheu, S. (2018). Decomposer diversity increases biomass production and shifts aboveground-belowground biomass allocation of common wheat. *Scientific Reports*, 8(1), 1-8.
- Erbaugh, J. T., Pradhan, N., Adams, J., Oldekop, J. A., Agrawal, A., Brockington, D., ... & Chhatre, A. (2020). Global forest restoration and the importance of prioritizing local communities. *Nature Ecology & Evolution*, 1-5.
- Faucon, M. P., Houben, D., & Lambers, H. (2017). Plant functional traits: soil and ecosystem services. *Trends in plant science*, 22(5), 385-394.
- Fern, K., Fern, A., Morris, R. (2014). Useful tropical plants database. Available online: <http://tropical.theferns.info/> (accessed on 16 October 2020).
- Fragoso, F. P., & Varanda, E. M. (2011). Flower-visiting insects of five tree species in a) restored area of semideciduous seasonal forest. *Neotropical entomology*, 40(4), 431-435.
- Fu, B., Zhang, L., Xu, Z., Zhao, Y., Wei, Y., & Skinner, D. (2015). Ecosystem

- services in changing land use. *Journal of Soils and Sediments*, 15(4), 833-843.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., ... & Mikusiński, G. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature communications*, 4(1), 1-8.
- Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., & Hättenschwiler, S. (2010). Diversity meets decomposition. *Trends in ecology & evolution*, 25(6), 372-380.
- González-Díaz, P., Ruiz-Benito, P., Gosalbez Ruiz, J., Chamorro, G., & Zavala, M. A. (2019). A Multifactorial Approach to Value Supporting Ecosystem Services in Spanish Forests and Its Implications in a Warming World. *Sustainability*, 11(2), 358.
- Greenslade, P. J. M. (1973). Sampling ants with pitfall traps: digging-in effects. *Insectes Sociaux*, 20(4), 343-353.
- Hand, K.L., Doick, K.J., and Moss, J.L. (2019). Ecosystem services delivery by large stature urban trees Research Report. *Forest Research, Edinburgh*. www.forestresearch.gov.uk/publications
- Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annual. Review. Ecology. Evolution. Systematics.*, 36, 191-218.
- Hawthorne, W., & Gyakari, N. (2006). Photoguide for the forest trees of Ghana: a tree-spotter's field guide for identifying the largest trees. *Oxford Forestry Institute*, Department of Plant Sciences.
- Hölting, L., Jacobs, S., Felipe-Lucia, M. R., Maes, J., Norström, A. V., Plieninger, T., & Cord, A. F. (2019). Measuring ecosystem multifunctionality across scales. *Environmental Research Letters*, 14(12), 124083.
- Jasaw, G. S., Saito, O., Gasparatos, A., Shoyama, K., Bofo, Y. A., & Takeuchi, K. (2017). Ecosystem services trade-offs from high fuelwood use for traditional shea butter processing in semi-arid Ghana. *Ecosystem services*, 27, 127-138.

- Kassambara, A. (2020). ggpubr: “ggplot2” Based Publication Ready Plots (Version 0.3. 0)[Computer software].
- Kearney, S. P., Fonte, S. J., García, E., Siles, P., Chan, K. M. A., & Smukler, S. M. (2019). Evaluating ecosystem service trade-offs and synergies from slash-and-mulch agroforestry systems in El Salvador. *Ecological indicators*, 105, 264-278.
- Kitz, F., Steinwandter, M., Traugott, M., & Seeber, J. (2015). Increased decomposer diversity accelerates and potentially stabilises litter decomposition. *Soil Biology and Biochemistry*, 83, 138-141.
- Kremen, C., M'Gonigle, L. K., & Ponisio, L. C. (2018). Pollinator community assembly tracks changes in floral resources as restored hedgerows mature in agricultural landscapes. *Frontiers in Ecology and Evolution*, 6, 170.
- Lafond, V., Cordonnier, T., Mao, Z., & Courbaud, B. (2017). Trade-offs and synergies between ecosystem services in uneven-aged mountain forests: evidences using Pareto fronts. *European Journal of Forest Research*, 136(5), 997-1012.
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., ... & Rossi, J. P. (2006). Soil invertebrates and ecosystem services. *European journal of soil biology*, 42, S3-S15.
- Lewis, S. L., Sonké, B., Sunderland, T., Begne, S. K., Lopez-Gonzalez, G., Van Der Heijden, G. M., ... & Bastin, J. F. (2013). Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1625), 20120295.
- Li, Z., Deng, X., Jin, G., Mohammed, A., & Arowolo, A. O. (2020). Trade-offs between agricultural production and ecosystem services: A case study in Zhangye, Northwest China. *Science of The Total Environment*, 707, 136032.
- Luck, G. W., Daily, G. C., & Ehrlich, P. R. (2003). Population diversity and ecosystem services. *Trends in Ecology & Evolution*, 18(7), 331-336.
- Luong, J. C., Turner, P. L., Phillipson, C. N., & Seltmann, K. C. (2019). Local

- grassland restoration affects insect communities. *Ecological Entomology*, 44(4), 471-479.
- Lyytimäki, J., & Sipilä, M. (2009). Hopping on one leg—The challenge of ecosystem disservices for urban green management. *Urban Forestry & Urban Greening*, 8(4), 309-315.
- Maldonado, M. B., Aranibar, J. N., Serrano, A. M., Chacoff, N. P., & Vázquez, D. P. (2019). Dung beetles and nutrient cycling in a dryland environment. *Catena*, 179, 66-73.
- Mander, Ü., Helming, K., & Wiggering, H. (2007). Multifunctional land use: meeting future demands for landscape goods and services. In *Multifunctional land use* (pp. 1-13). Springer, Berlin, Heidelberg.
- Manning, P., Slade, E. M., Beynon, S. A., & Lewis, O. T. (2016). Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. *Agriculture, Ecosystems & Environment*, 218, 87-94.
- Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F. T., Mace, G., ... & Fischer, M. (2018). Redefining ecosystem multifunctionality. *Nature, Ecology & Evolution*, 2, 427–436.
- Millennium ecosystem assessment, M. E. A. (2005). *Ecosystems and human well-being* (Vol. 5). Washington, DC: Island Press.
- Mori, A. S., Lertzman, K. P., & Gustafsson, L. (2017). Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *Journal of Applied Ecology*, 54(1), 12-27.
- Morrison, E. B., & Lindell, C. A. (2011). Active or passive forest restoration? Assessing restoration alternatives with avian foraging behaviour. *Restoration Ecology*, 19(201), 170-177.
- Nicholls, C. I., & Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable development*, 33(2), 257-274.
- Nunoo, I., Darko, B. O., & Owusu, V. (2015). Restoring degraded forest landscape for food security: Evidence from cocoa agroforestry systems,

- Ghana. *Enhancing food security through forest landscape restoration: Lessons from Burkina Faso, Brazil, Guatemala, Viet Nam, Ghana, Ethiopia and Philippines*, 122. Pais, M. P., & Varanda, E. M. (2010). Arthropod recolonization in the restoration of a semideciduous forest in southeastern Brazil. *Neotropical entomology*, 39(2), 198-206.
- Peña, L., Onaindia, M., Fernández de Manuel, B., Ametzaga-Arregi, I., & Casado-Arzuaga, I. (2018). Analysing the synergies and trade-offs between ecosystem services to reorient land use planning in metropolitan Bilbao (Northern Spain). *Sustainability*, 10(12), 4376.
- Powell, B., Thilsted, S. H., Ickowitz, A., Termote, C., Sunderland, T., & Herforth, A. (2015). Improving diets with wild and cultivated biodiversity from across the landscape. *Food Security*, 7(3), 535-554.
- Raudsepp-Hearne, C., Peterson, G. D., & Bennett, E. M. (2010). Ecosystem service bundles for analyzing trade-offs in diverse landscapes. *Proceedings of the National Academy of Sciences*, 107(11), 5242-5247.
- Reed, J., van Vianen, J., Foli, S., Clendenning, J., Yang, K., MacDonald, M., ... & Sunderland, T. (2017). Trees for life: The ecosystem service contribution of trees to food production and livelihoods in the tropics. *Forest Policy and Economics*, 84, 62-71.
- Reubens, B., Moeremans, C., Poesen, J., Nyssen, J., Tewoldeberhan, S., Franzel, S., ... & Muys, B. (2011). Tree species selection for land rehabilitation in Ethiopia: from fragmented knowledge to an integrated multi-criteria decision approach. *Agroforestry systems*, 82(3), 303-330.
- Santoro, A., Venturi, M., Bertani, R., & Agnoletti, M. (2020). A Review of the Role of Forests and Agroforestry Systems in the FAO Globally Important Agricultural Heritage Systems (GIAHS) Programme. *Forests*, 11(8), 860.
- Schmidt, M. H., Clough, Y., Schulz, W., Westphalen, A., & Tschardtke, T. (2006). Capture efficiency and preservation attributes of different fluids in pitfall traps. *The Journal of Arachnology*, 34(1), 159-162.
- Seymour, F., & Harris, N. L. (2019). Reducing tropical

- deforestation. *Science*, 365(6455), 756-757.
- Shimamoto, C. Y., Padiyal, A. A., da Rosa, C. M., & Marques, M. C. (2018). Restoration of ecosystem services in tropical forests: A global meta-analysis. *PloS one*, 13(12), e0208523.
- Soliveres, S., Van Der Plas, F., Manning, P., Prati, D., Gossner, M. M., Renner, S. C., ... & Birkhofer, K. (2016). Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature*, 536(7617), 456-459.
- Staab, M., & Schuldt, A. (2020). The influence of tree diversity on natural enemies—a review of the “enemies” hypothesis in forests. *Current Forestry Reports*, 1-17.
- Strobl, K., Kollmann, J., & Teixeira, L. H. (2019). Integrated assessment of ecosystem recovery using a multifunctionality approach. *Ecosphere*, 10(11), e02930.
- Systat Software (2010). Sigma Plot version 12.0. Systat Software, San Jose, California, U.S.A.
- Turkelboom, F., Leone, M., Jacobs, S., Kelemen, E., García-Llorente, M., Baró, F., ... & Thoonen, M. (2018). When we cannot have it all: Ecosystem services trade-offs in the context of spatial planning. *Ecosystem services*, 29, 566-578.
- UNCCD (United Nations Convention to Combat Desertification). (2014). Land degradation neutrality resilience at local, national and regional levels. Bonn, Germany: United Nations Convention to Combat Desertification.
- Underwood, E. C., & Quinn, J. F. (2010). Response of ants and spiders to prescribed fire in oak woodlands of California. *Journal of Insect Conservation*, 14(4), 359-366.
- Vandermeulen, S., Ramírez-Restrepo, C. A., Beckers, Y., Claessens, H., & Bindelle, J. (2018). Agroforestry for ruminants: a review of trees and shrubs as fodder in silvopastoral temperate and tropical production systems. *Animal Production Science*, 58(5), 767-777.
- Voeks, R. A., & Rahmatian, M. (2004). The providence of nature: Valuing

- ecosystem services. *International Journal of Environmental Science & Technology*, 1(2), 151-163.
- Wagner, S., Rigal, C., Liebig, T., Mremi, R., Hemp, A., Jones, M., ... & Preziosi, R. (2019). Ecosystem services and importance of common tree species in coffee-agroforestry systems: Local knowledge of small-scale farmers at Mt. Kilimanjaro, Tanzania. *Forests*, 10(11), 963.
- Waldron, A., Garrity, D., Malhi, Y., Girardin, C., Miller, D. C., & Seddon, N. (2017). Agroforestry can enhance food security while meeting other sustainable development goals. *Tropical Conservation Science*, 10, 1940082917720667.
- Weisse, M, and Goldman E. D. (2019). The World Lost a Belgium-Sized Area of Primary Rainforests Last Year. *World Resources Institute*, 26 Apr. 2019, www.wri.org/blog/2019/04/world-lost-belgium-sized-area-primary-rainforests-last-year. (accessed on 09 October 2020).
- Zemp, D. C., Ehbrecht, M., Seidel, D., Ammer, C., Craven, D., Erkelenz, J., ... & Kreft, H. (2019). Mixed-species tree plantings enhance structural complexity in oil palm plantations. *Agriculture, Ecosystems & Environment*, 283, 106564.
- Zeng, Y., Gou, M., Ouyang, S., Chen, L., Fang, X., Zhao, L., ... & Xiang, W. (2019). The impact of secondary forest restoration on multiple ecosystem services and their trade-offs. *Ecological Indicators*, 104, 248-258.

Chapter VII: General Discussion

This study presents the first assessment of biodiversity (plants and invertebrates) attributes, soil conditions and ecosystem services, comparing post-mining restoration forest with land-use types along a gradient from pre-disturbance, pre-restoration, alternative land-use to a natural forest in West Africa. The four research chapters (III-VI) focus on the level of success in biodiversity recovery and soil condition improvement of an active post-mine restoration project.

The first study (Chapter III) focused on the soil conditions of the different land-use types and their relationship with plants and biomass attributes. Chapter IV further broadens our understanding through a functional trait approach of strategies in different tree species for acquiring and utilising resources that affect plant fitness, reproduction, mortality and competition abilities in each land-use type. Chapter V presents the observed relationship between biodiversity attributes (e.g., the link between arthropods and plant components), arthropod trophic complexity and strategies used for resource acquisition. The final Chapter (VI) assesses the possible trade-offs and synergies between ecosystem service proxies across land-use types. Here, I provides insight into the key findings of each chapter and their management implications for restoration activities with a focus on biodiversity and local human communities. I also provide recommendations for future research and restoration approaches and a critical discussion of some limitations of the study.

Main findings

1. Active forest restoration positively impacts soil conditions and related levels of above and below-ground biomass within 20 years: this study showed an improvement in soil conditions resembling those observed in the natural reference forest after active restoration (Chapter III). Except for bulk density, which was similar to the pre-restoration states (gravel site and agricultural field), the levels of most of the basic soil chemical properties (e.g., pH, N, P, K, Na, Ca, Mg, ECEC) resembled those of the natural reference forest, indicating a trajectory of

soils in the restored forest towards conditions in the natural forest.

The improved soil conditions after active forest restoration could be attributed to management decisions to use fast-growing tree species (e.g., *Senna siamea*) with extensive root distribution systems that can hold and stabilize disturbed loose soils after mining. In addition, adding tree species with the ability to fix atmospheric nitrogen (e.g., *Leucaena leucocephala*) helped improve the soil conditions in the restored forest. These mixes of tree species influenced the quality and content of organic materials and subsequently affected the composition of microbial communities for nutrient cycling (Pietrzykowski, 2019). Through facilitation and resource partitioning, using mixed tree species in post-mining restoration remains a viable option for ecological succession, and the successful establishment of tree communities is hence essential for facilitating soil development after disturbance (Macdonald et al., 2015). The high soil bulk density in the restored forest could reflect the lingering effects of compaction from heavy machinery during the mining era. Soils with high bulk density affect infiltration rates, rooting depth penetration, available water capacity, and the activities of soil microorganisms, affecting soil productivity (Strock et al., 2022; Li et al., 2002). This issue could be improved over time through reduced tillage coupled with planting mixed tree species with different rooting depths (Hobson et al., 2021; Schlüter et al., 2018).

2. Plant communities and soil properties drive ecosystem multifunctionality:

the functional structure parameters (composition and diversity of forest communities) driving ecosystem multifunctionality showed comparable variability among the three forest ecosystems (Chapter IV). Ecosystem services and multifunctionality were best explained by the differences between the site conditions (soil and tree communities), with the functional richness of tree communities providing additional explanatory power independent of the selected ecosystem. The highest functional space for ecosystem services was shared by the natural and restored forest and was mainly driven by carbon storage, invertebrate activities and decomposition rates. These results could be explained

by the fact that these two ecosystems share similar volumes of above-ground biomass, organic root carbon and soil properties resulting from previous management activities, especially in the restored forest. The observed similarity between the restored and natural forest could be explained by the fertile soil conditions of both ecosystems, which might have translated into higher tree species diversity and the respective functional attributes, subsequently enhancing productivity (carbon storage potential; Måren & Sharma, 2021; Kothandaraman et al., 2020). Ultimately, the ability of each forest type to perform multiple ecosystem functions simultaneously (multifunctionality) depends on their functional richness driven by the local soil conditions (Huang et al., 2019; Thompson & Gonzalez, 2016).

3. Active forest restoration improves habitat conditions, promotes resource availability and creates diversified ecological niches for arthropod communities: the composition of arthropod communities differs between land-use types and seasons based on the degree to which resources (habitat and food) are available for arthropods. We observed a diverse tree community and higher volumes of deadwood in the tree land-use types (agroforestry plantation, restored and natural forests) than in the historical land-use type (unrestored former gravel mine land and agricultural fields; Chapter V), explaining part of the observed variation between arthropod communities across the land-use types. Arthropod activity density was significantly lower at the unrestored former gravel site and was not comparable to levels in the natural forest, the restored forest and the agroforestry plantation. All the forest systems had some dominant groups, such as Blattodea, Julida, Hymenoptera, Coleoptera and Araneae, independent of the season. For arthropod community composition, the restored forest was completely distinct from the gravel site and had an intermediate position between the agroforestry plantation and the natural forest, indicating some success in restoring arthropod communities with the restoration intervention. This is best explained by the diverse plant communities or the heterogeneous structure of tree communities across the land-use types. Diverse plant communities are more productive (Allan

et al., 2011; Tilman et al., 2001), provide a larger number of niche opportunities (Rutten et al., 2021) and supply more resources for arthropods (Schuldt et al., 2019). According to the habitat heterogeneity hypothesis (MacArthur, 1972), heterogeneous plant communities increase the availability of ecological niches, which facilitate the co-existence of many species (McClain & Barry, 2010) with cascading effects on ecosystem functioning (Tao et al., 2019). Deadwood and litter components in the forest land-use types offer important microhabitat and food resources for predaceous arthropods and their associated prey (Mhlanga et al., 2022; Dufour-Pelletier et al., 2020). Thus, both structure- and resource-mediated effects affect arthropod communities across the different land-use types (Diehl et al., 2013).

Similarly, spider communities were taxonomically richer in the restored and natural forests than in the agroforestry system and the gravel site. These differences could be attributed to the variation in vegetation structure, prey availability and abiotic conditions defining food and habitat resources for spiders and their prey (Müller et al., 2022; Rosa et al., 2018; Yamazaki et al., 2017). The characteristic complex vegetation attributes of the restored and natural forests should offer a wider range of prey (Diehl et al., 2013) as well as more diverse niches for spiders (Stańska et al., 2018; Cardoso et al., 2011).

For beetle communities, a significant difference in activity density was observed between the land-use types with trees and the gravel site, but even within the forest types. Among forest types, the restored forest recorded the lowest activity density compared to the agroforestry plantation and the natural forest. A possible explanation could be the dominance of non-native tree species, e.g., *Tectona grandis* and *Senna siamia*, as well as its succession stage. This confirms the results of a previous study (e.g., Fischer & Lindenmayer, 2007) that observed a lower beetle diversity in a non-native young forest plantation compared to an old-native forest. Old native forests are usually characterized by higher arthropod diversity because of their stable climatic conditions, higher plant species richness providing food resources and their structural complexity enhancing the habitat needs of beetles (Schowalter, 2017).

4. Seasonal conditions drive arthropod communities across land-use types:

in addition to productivity and structure-mediated effects, seasonality also played a major role in shaping arthropod communities by influencing plant resource distribution and concentration for most arthropod groups in our study. Pronounced seasonal variations that characterize tropical rain forests determine the quality and quantity of resources available at a particular period for arthropod activities (Basset et al., 2015). Most arthropod taxonomic groups in this study showed a higher activity density in the wet season, reflecting the concentration of resources available for arthropods (da Silva et al., 2011). Water and light available in the wet season allow plants to flush young leaves as an important resource for herbivorous arthropods (Richards & Windsor, 2007). In addition, the wet season might have facilitated the emergence of arthropods from the soil and the development of large patches of potential host plants (Basset et al., 2015). The higher activity density of predatory arthropods (e.g., spiders) recorded in our study in the wet season could probably be the result of the increased activity density of other arthropods serving as prey for spiders (Dennis et al., 2015). Wardhaugh et al. (2018) observed a strong seasonal variation in beetle communities driven by temperature and peaking in the summer wet season in a tropical rainforest. Similarly, in a neotropical rainforest, significant seasonal variation in Diptera (Corethrellidae) communities was observed with a peak breeding period in the rainy season (Legett et al., 2018). Depending on the land-use type (e.g., farmland), pronounced seasonal fluctuations were also observed for butterfly communities in a Western African dryland ecosystem (Schmitt et al., 2021). The lower activity density of arthropod communities observed in this study in the dry season could be attributed to a long period of drought conditions coupled with water stress, which might have induced physiological constraints on plants, thereby limiting plant resources essential for arthropod activities (Huberty & Denno, 2004).

5. Levels of proxy-based ecosystem services differed between forest types, with optimal levels provided by the natural forest: different levels of ecosystem services were observed for each forest type, with optimal levels provided only by the natural and the restored forest holding an intermediate position between the natural forest and the agroforestry plantation (Chapter VI). The differences in the levels of ecosystem service provisioning could be attributed to the management strategies that influenced tree species composition in each forest. The specific properties of individual tree species translate into different levels of ecosystem services (Gamfeldt et al., 2013).

The tree species composition in the restored forest consisted of about 30 % of exotic species. The agroforestry consisted of a mixture of exotic and indigenous tree species, with only indigenous species characterizing the natural forest (Chapter III). Tree species were significantly more diverse in the natural forest than in the restored and agroforestry systems (Chapter V). Forest management for agroforestry and restoration focused on planting a few tree species with the ability to stabilize and improve soil conditions or provide food and fuelwood for local human communities, with little focus on species that could improve carbon storage potential or enhance the activities of ecosystem service providing organisms. Forest management practices in both the restored forest and the agroforestry plantation hence limited the provision of biodiversity-based ecosystem functions due to the type of tree species selected for restoration activities. Numerous studies have discussed the species-biodiversity-ecosystem service relationship. For instance, the conversion of pine to spruce plantations resulted in negative consequences for biodiversity (e.g., pest and pathogen outbreaks) and many ecosystem services (e.g., trade-offs; Felton et al., 2020). More diverse tree communities provide higher levels of multiple ecosystem services in northern Europe (e.g., biomass production, game production potential, soil carbon storage and berry production; Gamfeldt et al., 2013).

6. Synergetic relationships with no apparent trade-offs between pairs of ecosystem service proxies in the different forest types: synergies are observed when the provision of one service goes along with higher levels of another service (Berry et al., 2020). An increase in the levels of one ecosystem service that relates to a decrease in another ecosystem service results in trade-offs (Lafond et al., 2017; Birkhofer et al., 2015; Bennett et al., 2009). Most restoration programs, however, aim at the simultaneous enhancement of more than one ecosystem service and try to avoid trade-offs, thereby creating synergies to meet the diverse needs of society (Birkhofer et al., 2019; Zeng et al., 2019).

Five of the fourteen possible relationships observed between ecosystem services in our study were significantly positive (synergies) with no observed trade-offs (Chapter VI). We observed a simultaneous increase in food tree biomass with increasing numbers of decomposing arthropods, confirming the synergy between supporting (soil formation) services and food provisioning. Decomposing organisms usually reduces soil compaction, increases soil aeration and facilitates the breakdown of organic materials into more elementary substances useful for food production (Ravn et al., 2020; Whalen, 2014).

In addition, decomposing organisms accelerate litter decomposition and remobilize nutrients for food production (Maldonado et al., 2019; Eisenhauer et al., 2018). Similarly, fodder tree biomass also correlated positively with the numbers of predaceous arthropods resulting from the development of a wider niche range in fodder tree communities.

Conclusion

In addressing deforestation in Afrotropical regions, it is evident that active forest restoration provides a sustainable option to minimize the impact on biodiversity and ecosystem service provision to local communities. This study revealed an improvement in soil conditions to levels comparable to the states observed in the undisturbed natural forest after two decades of active forest restoration. This successful trajectory was facilitated by the use of potted seedlings with fresh topsoil, which served as suitable soil nuclei in creating an optimal microclimate that overcame potential constraints emanating from mining-induced disturbances. Even though restoration efforts most commonly promote the establishment of native tree species, our study highlights that the use of fast-growing exotic tree species coupled with their extensive root distribution systems provided support for soil formation and the development of vegetation cover. This limited the impacts of soil erosion associated with mining and increased the carbon sequestration potential by both above and below-ground biomass.

Forest ecosystems with higher functional diversity were superior in providing multiple ecosystem services simultaneously, confirming the positive role of plant communities in driving ecosystem functioning and multifunctionality. Overall, we observed several synergies between ecosystem services with no apparent trade-offs. In addition, these diverse plant communities further support rich arthropod communities by providing food and habitat resources.

Comparing biodiversity attributes and ecosystem services between land-use types, the restored forest mostly took an intermediate position between the natural forest and the agroforestry plantation and often resembled the natural forest more, indicating a successful restoration trajectory after 20 years. The active forest restoration approach is more promising than agroforestry in restoring tree and arthropod biodiversity towards a state that resembles the natural forest. Leaving former mining sites unmanaged is not a sustainable option for restoration targeting biodiversity and ecosystem service recovery, as communities were poor and did not resemble the natural reference forest.

This research improves our understanding of how an active restoration

approach can improve soil conditions, biodiversity and ecosystem service provision compared to pre-and post-disturbance and a reference state. As a result, we recommend the future refinement of restoration approaches and management strategies tailored to enhance functional diversity for both tree and arthropod communities and soil properties for maximum ecosystem service provision. Table 1 presents an overview of the levels of biodiversity and ecosystem services assessed for all the land-use types.

Table 1: Levels of biodiversity attributes and ecosystem services across land-use types. Chapter(s) each attribute was studied are indicated

Attributes	Land-use types					Remarks	Chapter
	AG	GS	AF	RF	NF		
Tree communities							
Species and functional diversity	-	-	++	++	+++	Tree communities were more diverse in NF compared to RF and AF	III, IV, V, VI
Arthropod communities							
Activity density	-	+	++	+++	+++	Arthropod activity density were higher for NF and RF than AF and GS	IV, V, VI
Ecological processes							
Soil nutrients	++	+	++	++	+++	Soil conditions were better in NF, RF, and AF than AG and GS	III, IV
Carbon storage	-	-	+++	++	+++	Carbon storage was significantly higher in NF and AF than RF	III, IV, VI
Ecosystem service proxies							
Food tree biomass	-	-	+++	++	+++	Food tree biomass was higher in NF and AF than RF	VI
Fodder tree biomass	-	-	++	+++	+++	Fodder tree biomass was lower in AF than RF and NF	VI
Fuelwood biomass	-	-	++	++	+++	Fuelwood biomass was higher in NF than FR and AF	VI
Medicinal tree biomass	-	-	++	+++	+++	Medicinal tree biomass was higher in NF than RF and AF	VI
Mulch tree biomass	-	-	+	++	+++	Mulch tree biomass was higher in NF than RF and AF	VI
Decomposers	-	-	++	+++	+++	NF had higher decomposers than FR and AF	IV, V, VI
Predators	-	-	++	+++	+++	RF had higher predators than NF and AF	IV, V, VI

NB: - (no records), +(High/good), ++(Higher/better), +++ (Highest/best)

References

- Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., & Hillebrand, H. (2011). More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences*, *108*(41), 17034–17039. <https://doi.org/10.1073/pnas.1104015108>
- Basset, Y., Cizek, L., Cuénoud, P., Didham, R. K., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A. K., Schmidl, J., Winchester, N. N., Roubik, D. W., Aberlenc, H.-P., Bail, J., Barrios, H., Bridle, J. R., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte da Rocha, W., ... Leponce, M. (2015). Arthropod Distribution in a Tropical Rainforest: Tackling a Four Dimensional Puzzle. *PLOS ONE*, *10*(12), e0144110. <https://doi.org/10.1371/journal.pone.0144110>
- Bennett, E. M., Peterson, G. D., & Gordon, L. J. (2009). Understanding relationships among multiple ecosystem services: Relationships among multiple ecosystem services. *Ecology Letters*, *12*(12), 1394–1404. <https://doi.org/10.1111/j.1461-0248.2009.01387.x>
- Berry, Z. C., Jones, K. W., Gomez Aguilar, L. R., Congalton, R. G., Holwerda, F., Kolka, R., Looker, N., Lopez Ramirez, S. M., Manson, R., Mayer, A., Muñoz-Villers, L., Ortiz Colin, P., Romero-Urbe, H., Saenz, L., Von Thaden, J. J., Vizcaíno Bravo, M. Q., Williams-Linera, G., & Asbjornsen, H. (2020). Evaluating ecosystem service trade-offs along a land-use intensification gradient in central Veracruz, Mexico. *Ecosystem Services*, *45*, 101181. <https://doi.org/10.1016/j.ecoser.2020.101181>
- Birkhofer, K., Addison, M. F., Arvidsson, F., Bazelet, C., Bengtsson, J., Booyesen, R., Conlong, D., Haddad, C., Janion-Scheepers, C., Kapp, C., Lindborg, R., Louw, S., Malan, A. P., Storey, S. G., Swart, W. J., & Addison, P. (2019). Effects of Ground Cover Management on Biotic Communities, Ecosystem Services and Disservices in Organic Deciduous Fruit Orchards in South Africa. *Frontiers in Sustainable Food Systems*, *3*, 107. <https://doi.org/10.3389/fsufs.2019.00107>

-
- Birkhofer, K., Smith, H. G., Weisser, W. W., Wolters, V., & Gossner, M. M. (2015). Land-use effects on the functional distinctness of arthropod communities. *Ecography*, 38(9), 889–900. <https://doi.org/10.1111/ecog.01141>
- Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global Patterns of Guild Composition and Functional Diversity of Spiders. *PLoS ONE*, 6(6), e21710. <https://doi.org/10.1371/journal.pone.0021710>
- da Silva, E. V., Bouillet, J.-P., de Moraes Gonçalves, J. L., Junior, C. H. A., Trivelin, P. C. O., Hinsinger, P., Jourdan, C., Nouvellon, Y., Stape, J. L., & Laclau, J.-P. (2011). Functional specialization of Eucalyptus fine roots: Contrasting potential uptake rates for nitrogen, potassium and calcium tracers at varying soil depths: Functional specialization of Eucalyptus fine roots. *Functional Ecology*, 25(5), 996–1006. <https://doi.org/10.1111/j.1365-2435.2011.01867.x>
- Dennis, P., Skartveit, J., Kunaver, A., & McCracken, D. I. (2015). The response of spider (Araneae) assemblages to structural heterogeneity and prey abundance in sub-montane vegetation modified by conservation grazing. *Global Ecology and Conservation*, 3, 715–728. <https://doi.org/10.1016/j.gecco.2015.03.007>
- Diehl, E., Sereda, E., Wolters, V., & Birkhofer, K. (2013). Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: A meta-analysis. *Journal of Applied Ecology*, 50(1), 262–270. <https://doi.org/10.1111/1365-2664.12032>
- Dufour-Pelletier, S., A. Tremblay, J., Hébert, C., Lachat, T., & Ibarzabal, J. (2020). Testing the Effect of Snag and Cavity Supply on Deadwood-Associated Species in a Managed Boreal Forest. *Forests*, 11(4), 424. <https://doi.org/10.3390/f11040424>
- Eisenhauer, N., Vogel, A., Jensen, B., & Scheu, S. (2018). Decomposer diversity increases biomass production and shifts aboveground-belowground biomass allocation of common wheat. *Scientific Reports*, 8(1), 17894. <https://doi.org/10.1038/s41598-018-36294-3>
- Felton, A., Petersson, L., Nilsson, O., Witzell, J., Cleary, M., Felton, A. M.,

-
- Björkman, C., Sang, Å. O., Jonsell, M., Holmström, E., Nilsson, U., Rönnerberg, J., Kalén, C., & Lindbladh, M. (2020). The tree species matters: Biodiversity and ecosystem service implications of replacing Scots pine production stands with Norway spruce. *Ambio*, *49*(5), 1035–1049. <https://doi.org/10.1007/s13280-019-01259-x>
- Fischer, J., & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: A synthesis. *Global Ecology and Biogeography*, *16*(3), 265–280. <https://doi.org/10.1111/j.1466-8238.2007.00287.x>
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Fröberg, M., Stendahl, J., Philipson, C. D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., & Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, *4*(1), 1340. <https://doi.org/10.1038/ncomms2328>
- Hobson, D., Harty, M., Tracy, S., & McDonnell, K. (2021). *The effect of tillage depth and traffic management on soil properties and root development during two growth stages of winter wheat (Triticum aestivum L.)* [Preprint]. Soil degradation (chemical, physical and biological). <https://doi.org/10.5194/soil-2021-129>
- Huang, X., Su, J., Li, S., Liu, W., & Lang, X. (2019). Functional diversity drives ecosystem multifunctionality in a *Pinus yunnanensis* natural secondary forest. *Scientific Reports*, *9*(1), 6979. <https://doi.org/10.1038/s41598-019-43475-1>
- Huberty, A. F., & Denno, R. F. (2004). Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*, *85*(5), 1383–1398. <https://doi.org/10.1890/03-0352>
- Kothandaraman, S., Dar, J. A., Sundarapandian, S., Dayanandan, S., & Khan, M. L. (2020). Ecosystem-level carbon storage and its links to diversity, structural and environmental drivers in tropical forests of Western Ghats, India. *Scientific Reports*, *10*(1), 13444. <https://doi.org/10.1038/s41598-020-70313-6>
-

- Lafond, V., Cordonnier, T., Mao, Z., & Courbaud, B. (2017). Trade-offs and synergies between ecosystem services in uneven-aged mountain forests: Evidences using Pareto fronts. *European Journal of Forest Research*, 136(5–6), 997–1012. <https://doi.org/10.1007/s10342-016-1022-3>
- Legett, H. D., Baranov, V. A., & Bernal, X. E. (2018). Seasonal variation in abundance and diversity of eavesdropping frog-biting midges (Diptera, Corethrellidae) in a neotropical rainforest. *Ecological Entomology*, 43(2), 226–233. <https://doi.org/10.1111/een.12492>
- Li, C. H., Ma, B. L., & Zhang, T. Q. (2002). Soil bulk density effects on soil microbial populations and enzyme activities during the growth of maize (*Zea mays* L.) planted in large pots under field exposure. *Canadian Journal of Soil Science*, 82(2), 147–154. <https://doi.org/10.4141/S01-026>
- MacArthur, R. H. (1972). Geographical ecology: Patterns in the distribution of species. In N. Y. Haper & E. O. Wilson (Eds.), *The theory of island biogeography*. Princeton Univ. Press.
- Macdonald, K., Lund, M., & Blanchette, M. (2015). *Impacts of Artisanal Small-Scale Gold Mining on Water Quality of a Tropical River (Surow River, Ghana)*. 12.
- Maldonado, M. B., Aranibar, J. N., Serrano, A. M., Chacoff, N. P., & Vázquez, D. P. (2019). Dung beetles and nutrient cycling in a dryland environment. *CATENA*, 179, 66–73. <https://doi.org/10.1016/j.catena.2019.03.035>
- Måren, I. E., & Sharma, L. N. (2021). Seeing the wood for the trees: Carbon storage and conservation in temperate forests of the Himalayas. *Forest Ecology and Management*, 487, 119010. <https://doi.org/10.1016/j.foreco.2021.119010>
- McClain, C. R., & Barry, J. P. (2010). Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology*, 91(4), 964–976. <https://doi.org/10.1890/09-0087.1>
- Mhlanga, L., Kapembeza, C., Sithole, R., & Kativu, S. (2022). Variation in ground insect diversity, composition and abundance across land use types in an African savanna, Zimbabwe. *Scientific African*, 16, e01204.

- <https://doi.org/10.1016/j.sciaf.2022.e01204>
- Müller, J., Brandl, R., Cadotte, M. W., Heibl, C., Bässler, C., Weiß, I., Birkhofer, K., Thorn, S., & Seibold, S. (2022). A replicated study on the response of spider assemblages to regional and local processes. *Ecological Monographs*. <https://doi.org/10.1002/ecm.1511>
- Pietrzykowski, M. (2019). Tree species selection and reaction to mine soil reconstructed at reforested post-mine sites: Central and eastern European experiences. *Ecological Engineering*, 142, 100012. <https://doi.org/10.1016/j.ecoena.2019.100012>
- Ravn, N. R., Michelsen, A., & Reboleira, A. S. P. S. (2020). Decomposition of Organic Matter in Caves. *Frontiers in Ecology and Evolution*, 8, 554651. <https://doi.org/10.3389/fevo.2020.554651>
- Richards, L. A., & Windsor, D. M. (2007). Seasonal variation of arthropod abundance in gaps and the understorey of a lowland moist forest in Panama. *Journal of Tropical Ecology*, 23(2), 169–176. <https://doi.org/10.1017/S0266467406003907>
- Rosa, M. G. da, Santos, J. C. P., Brescovit, A. D., Mafra, Á. L., & Baretta, D. (2018). Spiders (Arachnida: Araneae) in Agricultural Land Use Systems in Subtropical Environments. *Revista Brasileira de Ciência Do Solo*, 42(0). <https://doi.org/10.1590/18069657rbcs20160576>
- Rutten, G., Hönig, L., Schwaß, R., Braun, U., Saadani, M., Schuldt, A., Michalski, S. G., & Bruelheide, H. (2021). More diverse tree communities promote foliar fungal pathogen diversity but decrease infestation rates per tree species in a subtropical biodiversity experiment. *Journal of Ecology*, 109(5), 2068–2080. <https://doi.org/10.1111/1365-2745.13620>
- Schlüter, S., Großmann, C., Diel, J., Wu, G.-M., Tischer, S., Deubel, A., & Rücknagel, J. (2018). Long-term effects of conventional and reduced tillage on soil structure, soil ecological and soil hydraulic properties. *Geoderma*, 332, 10–19. <https://doi.org/10.1016/j.geoderma.2018.07.001>
- Schmitt, T., Ulrich, W., Delic, A., Teucher, M., & Habel, J. C. (2021). Seasonality and landscape characteristics impact species community structure and

- temporal dynamics of East African butterflies. *Scientific Reports*, 11(1), 15103. <https://doi.org/10.1038/s41598-021-94274-6>
- Schowalter, T. (2017). Arthropod Diversity and Functional Importance in Old-Growth Forests of North America. *Forests*, 8(4), 97. <https://doi.org/10.3390/f8040097>
- Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Buchmann, N., Durka, W., Fichtner, A., Fornoff, F., Härdtle, W., Hertzog, L. R., Klein, A.-M., Roscher, C., Schaller, J., von Oheimb, G., Weigelt, A., Weisser, W., Wirth, C., ... Eisenhauer, N. (2019). Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communications*, 10(1), 1460. <https://doi.org/10.1038/s41467-019-09448-8>
- Stańska, M., Stański, T., Wielgosz, E., & Hajdamowicz, I. (2018). Impact of Habitat Complexity on Body Size of Two Spider Species, *Alopecosa cuneata* and *A. pulverulenta* (Araneae, Lycosidae). In River Valley Grasslands. *Polish Journal of Environmental Studies*, 27(2), 853–859. <https://doi.org/10.15244/pjoes/75806>
- Strock, C. F., Rangarajan, H., Black, C. K., Schäfer, E. D., & Lynch, J. P. (2022). Theoretical evidence that root penetration ability interacts with soil compaction regimes to affect nitrate capture. *Annals of Botany*, 129(3), 315–330. <https://doi.org/10.1093/aob/mcab144>
- Tao, Y., Wang, Z., Ma, C., He, H., Xu, J., Jin, Y., Wang, H., & Zheng, X. (2019). Vegetation Heterogeneity Effects on Soil Macro-Arthropods in an Alpine Tundra of the Changbai Mountains, China. *Plants*, 8(10), 418. <https://doi.org/10.3390/plants8100418>
- Thompson, P. L., & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, 97(10), 2867–2879. <https://doi.org/10.1002/ecy.1502>
- Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and Productivity in a Long-Term Grassland Experiment. *Science*, 294(5543), 843–845. <https://doi.org/10.1126/science.1060391>

- Wardhaugh, C. W., Stone, M. J., & Stork, N. E. (2018). Seasonal variation in a diverse beetle assemblage along two elevational gradients in the Australian Wet Tropics. *Scientific Reports*, 8(1), 8559. <https://doi.org/10.1038/s41598-018-26216-8>
- Whalen, J. K. (2014). Managing Soil Biota-Mediated Decomposition and Nutrient Mineralization in Sustainable Agroecosystems. *Advances in Agriculture*, 2014, 1–13. <https://doi.org/10.1155/2014/384604>
- Yamazaki, L., Vindica, V. F., Brescovit, A. D., Marques, M. I., & Battirola, L. D. (2017). Temporal variation in the spider assemblage (Arachnida, Araneae) in canopies of *Callisthene fasciculata* (Vochysiaceae) in the Brazilian Pantanal biome. *Iheringia. Série Zoologia*, 107(0). <https://doi.org/10.1590/1678-4766e2017019>
- Zeng, Y., Gou, M., Ouyang, S., Chen, L., Fang, X., Zhao, L., Li, J., Peng, C., & Xiang, W. (2019). The impact of secondary forest restoration on multiple ecosystem services and their trade-offs. *Ecological Indicators*, 104, 248–258. <https://doi.org/10.1016/j.ecolind.2019.05.00>

Appendices

- The data that support the findings of **Chapter III** are openly available in figshare at <https://doi.org/10.6084/m9.figshare.20237583.v1>
- The data that support the findings of **Chapter IV** are openly available in figshare at <https://doi.org/10.6084/m9.figshare.16754938.v1>
- The data that support the findings of **Chapter V** are openly available in figshare at <https://doi.org/10.6084/m9.figshare.16556211.v1>
- The data that support the findings of **Chapter VI** are openly available in figshare at <https://doi.org/10.6084/m9.figshare.14402120.v2>.

Acknowledgements

Completing this thesis would not have been possible without the guidance and the support of some individuals and institutions. To start with, I would like to express my special appreciation and thanks to my able and dedicated supervisor, Prof. Dr. Klaus Birkhofer (BTU), whose expertise, understanding, valuable guidance, scholarly input, patience and consistent encouragement added considerably to my graduate experience. It has been an honour working with you, and I appreciate all your contributions of time and ideas to make this thesis experience productive and stimulating. Again, thank you for always having an open door for spontaneous discussions. I also appreciate the supervision role and guidance of Dr. Enrique Garcia de la Riva and PD Dr. Udo Bröring (BTU); without them, most of the complicated and hard-to-follow lines of thought would not have been answered. Special thanks to Dr. El Aziz Djoudi, Dr. Roman Bucher (all BTU) and Dr. Danilo Harms (Centrum für Naturkunde (CeNak)) for your guidelines and directions in the study design and results interpretation.

This thesis would not have been possible without the permission of Newmont Ghana Gold Limited, the Forestry Commission of Ghana and the Terchire Community. Granting me access to the Terchire restoration site, Bosomkese and Asukese Forest reserves, the surrounding farmlands, and abandoned gravel sites gave birth to all the datasets used in this study; I appreciate your support and cooperation. My field campaigns were possible mainly due to the assistance and support of the following dedicated people: Ebenezer D. Djagbletey (PhD), Kwabena Adu-Bonnah, Raymond Ayepah, Joe Frimpong Appiah, Ernest Adofu, Clement Wulnye, Daniel Kwame Debrah, Agro Prince Pascal, Obed Owusu Addai, Richard Quashie, Collins Ayine Nsor (PhD), Markfred Mensah, Yaw Opoku Boateng, Solomon Danso-Ankamah, Gloria Djagbletey (PhD), Desmond Asare, Frederick Nyahe, Edward Debrah Wiafe (PhD), Emmanuel Opuni-Frimpong (PhD); I appreciate all your contributions in diverse ways.

The scholarship supports from the Katholischer Akademischer Ausländer Dienst (KAAD), and Deutscher Akademischer Austauschdienst (DAAD STIBET),

the fellowship award from the Society for Conservation Biology (Graduate Student Research Fellowship Awards), the research grants from the Rufford Foundation (Grant numbers 27866-1 and 33624-2), the logistic support from IDEA WILD, and the Conference Travel Grant from the BTU Graduate Research School (GRS) is greatly appreciated.

I am indebted to my PhD colleagues at the Department of Ecology (Chefor, Lanya, Benjamin, Claudia, Daniel, Esteban, Fredrik, Haggart, Michael, Sergio, Bartosz, Ingrid, Martha, and Harreit) and our able department secretaries (Susann and Coliette), the supportive laboratory assistants (Claudia and Linda) and both our former and current ERM PhD coordinators (Dr. Birte Seffert and Dr. Stella Gypser); your contributions in diverse ways made my PhD journey smooth and successful, thank you very much. Special thanks to all current and former students at BTU who helped with the laboratory work (Mahlet Degefu Awoke, Benjamin Schnerch, Adwoa Benewah Adu-Yeboah, Sarina Böttner, Christos Konstantinos Paxinos, Kwadwo Gyasi Asante, Julia Yeboah, Thomas Schunack, Michael Nagel, Tarek Hossain Raju, and Sherihan Aly). You all did marvellously well on this project, your efforts are really appreciated.

To my friends (Sandra Bögner, Dr. Bernard Frimpong, Dr. Henry Mensah, Dr. Paul Nsiah, Dr. Bedu-Addo, Dr. Bryant, Dr. Obiri-Yeboah, Dr. Ansong-Omari, Dr. David Swqordor Gaikpa, Jessica Amprako, Okofo-Boansi, Ebenezer Ntriakwa, Bernard Effah Nyarko, Kwabena Buabeng, Kingsley Ofofu, Kwame Ampadu, Kingsberg Acquah, Francis Boobi, Adomaa Kusi-Boadu, Ordartey Lamptey, Rahman, Osei, Livingston, Theodore, Ferdinand, and Philip), thanks for the diverse support throughout my studies. Special thanks to Awurade Nyankopon, Rev. Father Stephen Kwasi Duodu of the Ghana Catholic Community, and Rev. Father Max Cappabianca of the Katholische Studierendengemeinde – Berlin. I thank Prof. Dr. Thomas Raab for being my second examiner and apl. Prof. Dr. Manfred Wanner for being the chairperson for the examination committee.

Heartfelt thanks go out to members of my family who were equally important throughout my studies and development. My father (William Dampsey Gyasi) has been very influential in helping me recognize the desire to yarn for greater heights.

My mother (Patience Opokua- Larbi), has been an inspiration and a constant source of support and encouragement. Growing up with my three sisters (Vida Ntiamoah Gyasi, Anita Agyabeng Gyasi and Casandra Gyasi), forever wandering through the forest and amazed by nature, developed my interest in science and ecology, to be specific. To the entire Dampsey family of Akyem Abomosu, I say a big thank you to you all for your guidance, financial support, and encouragement

List of publications

1. **Damphey, F. G**^{1,2,3,4}, Opuni-Frimpong, E., Nsor, C. A., Addai, J., Debrah, D. K., Schnerch, B., ... & Korjus, H. (2022). Taxonomic and community composition of epigeal arthropods in monoculture and mixed tree species plantations in a deciduous forest of Ghana. *Journal of Forestry Research*, 1-13.
2. Bentsi-Enchill, F., **Damphey, F. G**^{3,4}, Pappoe, A. N. M., Ekumah, B., & Akotoye, H. K. (2022). Impact of anthropogenic disturbance on tree species diversity, vegetation structure and carbon storage potential in an upland evergreen forest of Ghana, West Africa. *Trees, Forests and People*, 8, 100238.
3. Asare, D., Ansong, M., Kyereh, B., **Damphey, F. G**^{2,3}, & Asante, W. A. (2022). Mining methods exert differential effects on species recruitment at artisanal small-scale mining sites in Ghana. *Heliyon*, e09434.
4. **Damphey, F. G**^{1,2,3,4}, Birkhofer, K., Oliveras Menor, I., & de la Riva, E. G. (2022). The Functional Structure of Tropical Plant Communities and Soil Properties Enhance Ecosystem Functioning and Multifunctionality in Different Ecosystems in Ghana. *Forests*, 13(2), 297.
5. **Damphey, F. G**^{1,2,3,4}, Frimpong, B. F., Debrah, D. K., Agro, P. P., & Wiawe, E. D. (2022). Vegetation attributes drive the taxonomic richness and functional composition of beetles and spiders in mountainous urban green spaces. *Energy, Ecology and Environment*, 1-13.
6. **Damphey, F. G**^{1,2,3,4}, Adofo, E., Duah-Gyamfi, A., Adusu, D., & Opuni-Frimpong, E. (2021). Logging effects on seedling regeneration and diversity in a tropical moist semi-deciduous forest in Ghana. *Geology, Ecology, and Landscapes*, 1-12.
7. Opuni-Frimpong, E., Gabienu, E., Adusu, D., Opuni-Frimpong, N. Y., & **Damphey, F. G**^{3,4} (2021). Plant diversity, conservation significance, and community structure of two protected areas under different governance. *Trees, Forests and People*, 4, 100082.
8. **Damphey, F. G**^{1,2,3,4}, de la Riva, E. G., & Birkhofer, K. (2021). 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. *Frontiers in Forests and Global Change*, 4, 47.

9. **Damphey, F. G.** ^{1,2,3,4}, Birkhofer, K., Nsiah, P. K., & de la Riva, E. G. (2020). Soil properties and biomass attributes in a former gravel mine area after two decades of forest restoration. *Land*, 9(6), 209.

1: designed the experiment; 2: conducted fieldwork; 3: analysed data; 4: wrote the first draft of the manuscript