

Article

Opposing Ecological Strategies Together Promote Biomass Carbon Storage in Homegardens Agroforestry of Southern Bangladesh

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Abstract: Exploration of the biodiversity–environmental factors–carbon storage relationships have been a central research question in the changing global climate over the last few decades. However, in comparison to other forest ecosystems, very few studies have been conducted in homegarden agroforestry plantations, which have a tremendous capacity to battle global climate change sustainably. We hypothesized that (i) soil organic matter content has both a direct and indirect effect on aboveground carbon storage through species richness, structural diversity, functional diversity (FD) and functional composition (FC); (ii) some facets of diversity (structural diversity, FD and FC) would be more important in linking species richness to aboveground carbon; (iii) species richness, FC, structural diversity and FD would have a positive impact on aboveground carbon storage (AGC) after considering the effect of soil fertility; and (iv) FC would have a greater effect on AGC than the other three components of biodiversity. These hypotheses were tested using structural equation modeling with field data obtained from 40 homesteads in southwestern Bangladesh. We observed that species richness, FC of maximum canopy height and structural diversity had significant effects on AGC, while soil organic matter and FD of wood density had an insignificant effect. Among the four biodiversity components, the structural diversity had a greater influence on AGC. Contrary to our hypothesis, soil fertility and species richness did not have a significant indirect effect on AGC through their mediators. These four components of biodiversity, along with soil organic matter together explained 49% of the variance in AGC. Our findings indicate that both niche complementarity and selection effects regulate AGC in homegardens, where the former theory had stronger control of AGC in homegardens. Therefore, we need to maintain not only the species diversity but also structural diversity (DBH) and functional composition (canopy height) for enhancing aboveground carbon storage on a sustainable basis in homegardens and other restoration programs under nature-based solution.



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1. Introduction

Understanding the relationship between biodiversity and ecosystem services, in particular carbon storage, has been a central research theme in ecology over the recent decades [1–3]. This is due to the ongoing loss of biodiversity and its impact on the carbon storage capacity of forest ecosystems [4]. However, in comparison to tropical, subtropical and temperate forests [1,2,5,6], few studies have investigated homegardens agroforestry systems with an emphasis on multiple aspects of biodiversity (species, functional trait diversity and structural diversity) [7,8]. Homegardens in the tropical and subtropical

countries are rich in biodiversity, with uneven ages and a stand multilayer structure that resembles a forest. They play an important role in climate change mitigation and adaptation by sequestering and storing atmospheric CO₂ as biomass and soil organic matter [9,10]. In addition to this regulatory service (carbon sequestration), it also provides provisional services, such as food, fodder, fuel wood, timber and other domestic products [11–13]. Thus, homegardens can be viewed as one of the key nature-based solutions for climate change mitigation and adaptation.

Multiple abiotic and biotic factors interact with each other in the forest ecosystem and affect carbon storage [5,14]. Among the abiotic factors, some crucial factors which are interlinked to other physical, chemical and biological factors related to soil can be viewed as a key indicator of soil productivity [15,16]. For example, soil organic matter enhances common soil properties, such as bulk density, composition, texture and water holding capacity, cation exchange capacity, nutrient cycling, nitrogen mineralization bacteria, dinitrogen fixation, mycorrhizae fungi and microbial biomass productivity [15–17]. As a result, organic matter plays a key role in plant productivity and hence in aboveground carbon storage. In the case of biotic factors, the multiple aspects of biodiversity—species diversity, structural diversity, functional diversity and composition—are commonly being used for assessing their effects on carbon storage in recent years [2,14]. These multiple aspects of diversity can also mediate the effect of organic matter content on aboveground carbon storage, as they are also influenced by organic matter content. Thus, by considering these abiotic and biotic influences in an integrated modeling framework (structural equation model, a robust approach that considers both direct, indirect and total effects of predictors on response), this enriches our understanding of the biodiversity–environmental factor–carbon relationship in the homegarden agroforestry systems.

Several theories have been developed to explain the relationship between biodiversity and carbon, of which niche complementarity and selection theories are mostly supported by the results of biodiversity–carbon studies in different habitats [2,18,19]. In a study on whether the species richness (count of species in a plot or community), functional diversity (variation of different traits between species, e.g., maximum canopy height, wood density) or structural diversity (variation of DBH in a plot or community) has a positive effect on carbon storage, the niche complementarity effect is assumed to be effective in carbon storage [2,7,20]. The explanation behind this assumption is that niche complementary theory assumes that the ecosystem carbon capacity is mostly determined by the diverse coexisting species, with their greater trait variation in a community [2,21]. For example, balancing light demanding species in the top canopy and shade tolerant species in the lower canopy to optimize light use efficiency will lead to overall community carbon gain [2,18,19,22]. On the other hand, if the functional composition of plant traits—the community weighted mean of traits—in a community or stand has a positive effect on carbon storage [2,22–24], the selection effect is assumed to be efficient. The selection effect assumes that among the coexisting species, the dominant species with key characteristics determine the carbon storage [2,22,24]. For instance, maximum canopy height, a key indicator of light interception [25] and of structural change reflecting the higher resource use capacity of a species than its neighbor in a community, determines community scale biomass allocation and carbon storage [2,22–24]. While dominant species with their high tissue quality (e.g., high wood density indicates higher investment of biomass in per unit structure), has a positive effect on aboveground biomass and therefore carbon storage [22].

Bangladesh is a downstream country of major rivers, with a vast flat plain of fertile soil favorable for plant growth, making it one of the world's richest homegardening countries [10,26]. There are about 4.5 million ha of tree cover area outside the designated forest area of Bangladesh, in which homegarden's contribution is predominant [26,27]. Every household in each village has a homegarden, which is a well-established land use system and is biologically diverse [28,29]. Most of the studies on homegardens in Bangladesh remain descriptive on the floristic, structure, uses and the relation between household and home garden characters, with more recent studies on the taxonomic diver-

sity and carbon storage [30,31]. In this study, we are focused on the understanding of the biodiversity–carbon relationship after accounting for the effect of soil organic matter as a proxy of soil fertility. We hypothesized that (i) soil organic matter content has both a direct and indirect effect on aboveground carbon storage through species richness, structural diversity, functional diversity and functional composition; (ii) some facets of diversity (structural diversity, functional diversity and functional composition) would be more important in linking species richness to aboveground carbon; (iii) all the four biodiversity components have a positive effect on aboveground carbon storage after considering the effect of soil fertility; and (iv) functional compositions have a greater effect on aboveground carbon storage compared to other biodiversity components.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Dighalia Upazila, Khulna district of Southwestern Bangladesh (Figure 1). The study area is primarily a flood plain land mass between 22.50° to 22.60° N latitude and 89.3° to 89.37° E longitude. The deltaic landscape of this region is mainly low (<10 m above average sea level), flat and fertile [32]. The average area of the homegarden over the study site is 0.05 ha [10]. It generally enjoys a tropical to subtropical monsoon climate with an average annual temperature of 26°C . January is the coolest month, and April is the hottest month in this region. The average annual rainfall for this region is 1986 mm (range: 1400–2600 mm) [32].

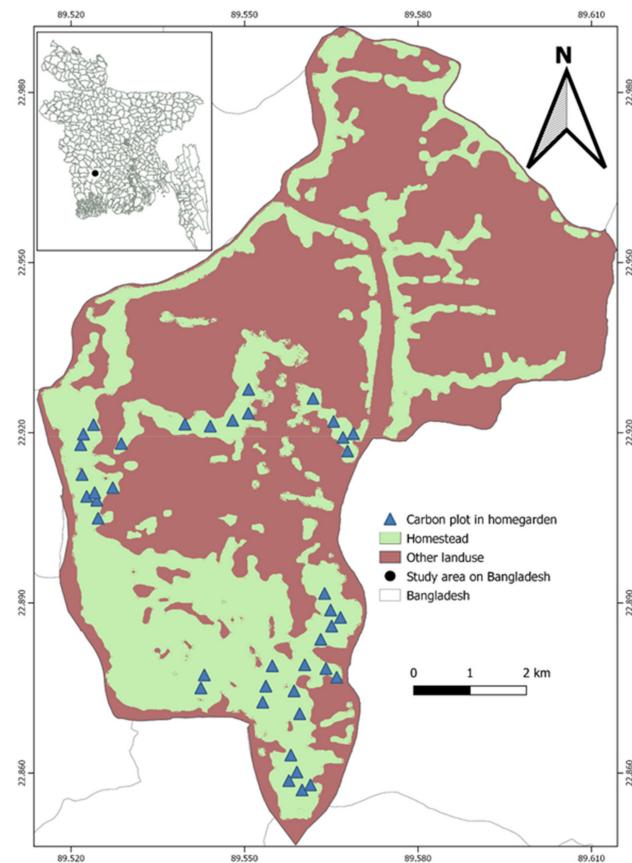


Figure 1. Location carbon plots within homesteads in Dighalia Upazila, Khulna, Bangladesh.

2.2. Field Inventory

We laid out 40 plots ($10\text{ m} \times 10\text{ m}$) at 40 household with homegardens in eight villages of Dighalia, Khulna, Bangladesh (Figure 1). The diameter and height of all the species having DBH (diameter at breast height) $\geq 3\text{ cm}$ were measured using diameter tape and a

range finder, respectively. All species in each sampled plot were identified and recorded to species level or by local name, and later were confirmed from an authentic source [10]. At each plot from the center, a 5 cm sample soil core was collected at the middle point of 0–15 cm soil depth that was pulled out using an open face peat auger. All samples were air-dried and then analyzed for soil organic content measurement at the Nutrient Dynamics Laboratory of Khulna University, Khulna, Bangladesh.

2.3. Data Analysis

Biomass Carbon

We used a common allometric equation for aboveground biomass estimation for trees because site-specific allometric equations were not available for all the species (38 species; Equation (1)) [33]. The wood density data were obtained from the Bangladesh Forest Research Institute [34] and Global Wood Density Database [35]. For species with missing wood density in these databases, we used community average wood density. The biomass of palm, coconut, betel nut and date species was estimated by using a height based allometric model (Equation (2)) [36]. We calculated biomass carbon by multiplying biomass with 0.5, as it is assumed that wood biomass contains 50% carbon [37].

$$\text{AGB (Mg/ha)} = \rho \times \exp (-1.499 + 2.148 \times \ln (\text{DBH}) + 0.207 \times (\ln (\text{DBH}))^2 - 0.0281(\ln (\text{DBH}))^3) \quad (1)$$

$$\text{AGB (Mg/ha)} = 6.666 + 12.826 \times \text{ht} \times 0.5 \times \ln(\text{ht}) \quad (2)$$

where AGB = aboveground biomass, ρ = wood density (g cm^{-3}), DBH = diameter at breast height, ht = H= height.

2.4. Functional Traits and Diversity Metrics

We used wood density and maximum canopy height, the two widely used functional traits in biodiversity–carbon relationship studies because they are highly related to aboveground biomass carbon [2,38]. Maximum canopy height for each tree species was extracted from field inventory data. We assessed species richness by counting the number of species in each plot. Plot level structural diversity was estimated by calculating standard deviation of DBH. Functional composition and functional diversity of traits were calculated using community weight mean (Equation (3)) and functional dispersion (Equation (4)) metric, respectively, in R by using FD package [39]. Both metrics were abundance weighted and the species wise total basal area in each plot was used as abundance because species contribution in an ecosystem is best represented by basal area [24,40]. As recommended, we standardized all the traits before calculating community weighted mean and functional dispersion.

$$\text{CWM}_{tj} = \sum_{i=1}^S P_{ij} t_i \quad (3)$$

where CWM_{tj} is the community weighted mean of trait t for j plot, S is the species richness, P_{ij} is the proportion of relative basal area of species i for j plot and t_i is the mean value of trait of species i .

$$\text{FDIS} = \frac{\sum a_j Z_j}{\sum a_j} \quad (4)$$

where a_j is the abundance of species j in terms of basal area and Z_j is the distance of species j to the weighted centroid c which represents the centroid of the n species in trait space.

For calculating soil organic matter, we used the Loss of Ignition method [41]. In this method, one gram of soil was taken in a pre-weighted porcelain cup and oven-dried at 105 °C for 24 h [41]. The oven-dried sample was ignited by using a digital muffle furnace

(WiseTherm F, Wisd, Korea) at 450 °C for four hours. After ignition and cooling at room temperature, we weighed the ashes to calculate the loss of ignition (Equation (5)).

$$\text{Loss of Ignition (\%)} = \frac{(W_{t105\text{ }^{\circ}\text{C}} - W_{t450\text{ }^{\circ}\text{C}})}{W_{t105\text{ }^{\circ}\text{C}}} \times 100 \quad (5)$$

Here, $W_{t105\text{ }^{\circ}\text{C}}$ is the weight of soil at 105 °C and $W_{t450\text{ }^{\circ}\text{C}}$ is the weight of soil at 450 °C.

2.5. Statistical Analysis

The structural equation model was used for assessing the direct, indirect and total effects of predictors on aboveground carbon storage [14,42–44]. The carbon taken up by plants and accumulated in plant biomass and soil organic matter over time is influenced by integrated mechanisms involving both abiotic and biotic influences [14,42,44]. For understanding the underlying mechanisms, simple linear or multiple linear regression is insufficient because they only provide insight into direct effects [43]. However, biotic and abiotic factors interact with each other and regulate ecosystem function and services jointly [14,42–44]. Thus, for addressing this complex system in an integrated way, we need to use complex modeling approaches, such as structural equation models [14,42–44]. Structural equation models are a robust approach (compared to multiple linear or bivariate relationships) that consider both the direct and indirect (through mediators) as well as the total effects (direct + indirect) of predictors [14,42–44]. All the biodiversity components, soil organic matter and aboveground carbon storage were log transformed and standardized for attaining linearity assumption before applying the structural equation model [43]. Analyses were performed using in R environment (Version 3.6.3) [45]. The structural equation models were employed using the Lavaan Package in [46] R for assessing the direct, indirect and total effects of soil nutrient, species richness, structural diversity and functional composition and functional diversity of maximum canopy height and wood density on aboveground carbon storage [43,47]. Based on our hypotheses, we started the structural equation model by including all the predictors and gradually removed the predictor which had high a p -value. We followed this process because multicollinearity among covariates may lead to the model dissatisfying the goodness of fit indices [42]. In the second structural equation model, we removed functional composition of wood density and in the third structural equation model we removed functional diversity of maximum canopy height (Supplementary Materials; Table S1). In the third structural equation model for assessing the effect of the predictors on aboveground carbon storage, the combination of soil organic matter, species richness, functional composition of maximum canopy height and functional diversity of wood density attained all the goodness of fit indices (Supplementary Materials; Table S1). The indirect effect of soil nutrient and species richness were calculated by multiplying the standardized effects of all the paths from them to aboveground carbon through different mediators [47]. The total effect of soil nutrient and species richness on aboveground carbon was estimated by summing the standardized direct and the standardized indirect effects [47]. We evaluated structural equation models by using different fit indices that are widely applied for structural equation models. For instance, we can assume that the structural equation model shows no significant deviation from the dataset if we found an insignificant chi-square test ($p > 0.05$), a comparative fit and Tucker–Lewis index with >0.90 and a standardized root mean square residual close to zero [47,48]. The standardized effect of each path of fitted SEMs was validated using a bootstrap (1000 times) resampling method using Lavaan package in R [46]. Furthermore, we applied multiple linear regression for quantifying the variance inflation factors for checking measure multicollinearity of the covariate in the final SEM, with a threshold value of two (Supplementary Materials; Table S2) [49]. We also applied a simple linear relationship for all the hypothesized paths of the final structural equation model for interpreting the result of the structural equation model [43].

3. Results

3.1. Bivariate Relationship between Different Predictors and Carbon Storage

Soil organic matter had an insignificant positive effect on aboveground carbon storage (Figure 2a; $p > 0.05$). Aboveground carbon was increased with all the biodiversity components except functional diversity of wood density (Figure 2b–e). However, among the four diversity components, structural diversity had the only significant effect on aboveground carbon storage (Figure 2b–e; $p < 0.05$). All the biodiversity components except functional composition of maximum canopy height showed an increasing trend with organic matter content, but none of the relationships were significant (Figure 2f,i, $p > 0.05$). Functional composition of maximum canopy height declined with species richness, while functional diversity of wood density increased with species richness (Figure 2j,l). Species richness also had an insignificant positive effect on structural diversity (variation of DBH; Figure 2k; $p > 0.05$).

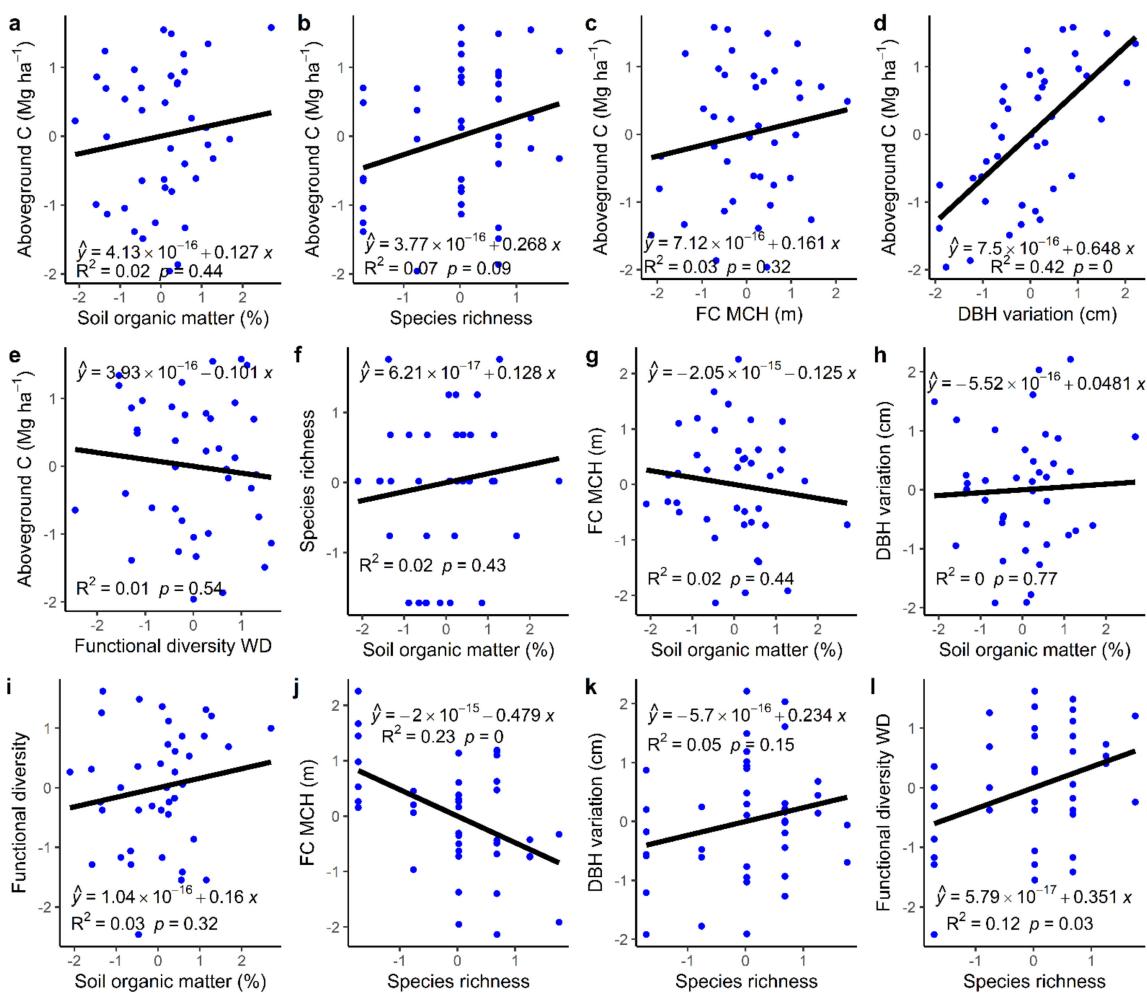


Figure 2. Bivariate relationship between predictors and response variables (all the direct paths of structural equation model in Figure 3). All the data were log transformed and standardized mean zero and one standard deviation. (a–e) Aboveground biomass carbon vs. soil organic matter (a), species richness (b), functional composition of maximum canopy height (FC MCH; (c)), variation of diameter at breast height (DBH at 1.37 m; (d)) and functional diversity of wood density (FC WD), respectively. (f–i) The effects of soil organic matter on species richness, FC MCH, variation of DBH and FC WD, respectively. (j–l) The effects of species richness on FC MCH, variation of DBH and FC WD, respectively.

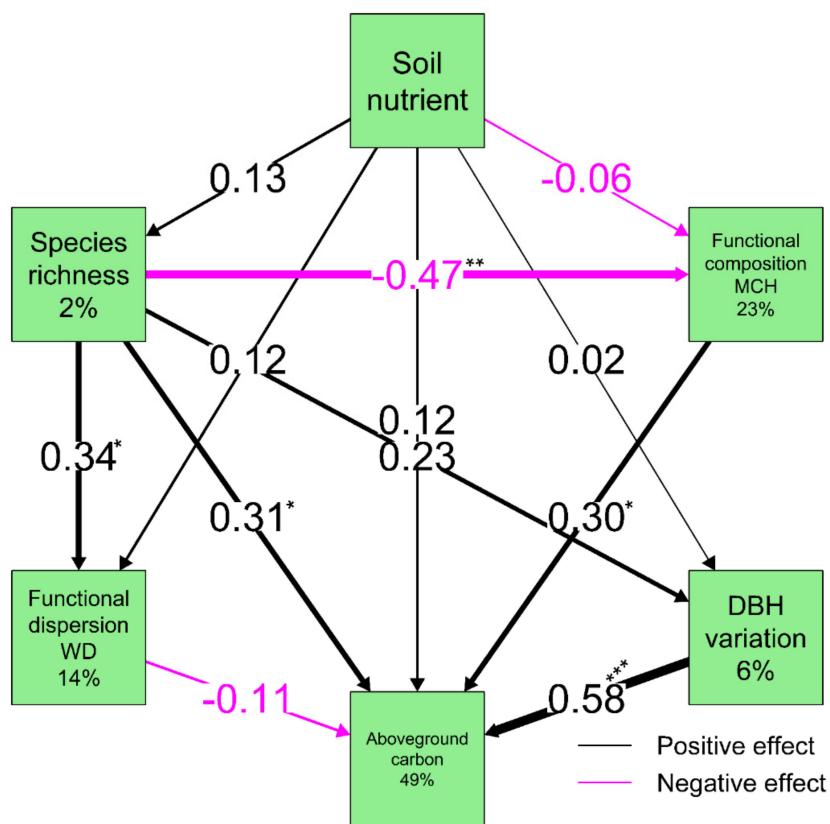


Figure 3. Underlying mechanism of the relationship between different components of biodiversity and aboveground carbon with structural equation modeling. The best fitted model with insignificant lower chi-square value ($\chi^2 = 2.198$, $p = 0.532$), along with comparative fit index (1) and Tucker–Lewis index (1) close to one and standardized root mean square residual close to zero (0.057), indicates no deviation of model from observed dataset and thus indicates good fit. The percentage value in the box of endogenous variables shows their explained variance (coefficient of determinant: R squared). The path values with a star mark indicates their significant level (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$), while the insignificant paths were indicated without a star mark ($p > 0.05$). MCH: maximum canopy height, WD: wood density and DBH: diameter at breast height (at 1.30 m).

3.2. Underlying Mechanism of Relationship between Soil Nutrient, Biodiversity and Carbon Storage

Soil organic matter had no direct and indirect effect on aboveground carbon storage (Figure 3; $p > 0.05$; Table 1). The effect of all biodiversity components (except functional diversity of wood density) on aboveground carbon stock were significant and positive (Figure 3; $p < 0.05$). Although functional composition of maximum canopy height partly mediated species richness effect on aboveground carbon storage (Figure 3), it was not retained when we validated it with bootstrapping (Table 1). Structural diversity had a strong effect on aboveground carbon, although it was not affected by soil organic matter and species richness (Figure 3; Table 1). Functional diversity of wood density had no effect on aboveground carbon storage, although it was positively influenced by species richness (Figure 3; Table 1).

Both soil organic matter and species richness had no total effect on aboveground carbon, we also did not find any significant effect ($p > 0.05$; Table 1).

The four biodiversity components along with the effect of soil organic matter in combination explained 49% of the variation of aboveground carbon stock ($R^2 = 0.49$). This is while the soil organic matter and species richness together explained 23% ($R^2 = 0.23$), 6% ($R^2 = 0.06$) and 14% ($R^2 = 0.06$) of functional composition of maximum canopy height, structural diversity and functional diversity of wood density, respectively (Figure 3). Soil nutrient also explained 2% of the variation of species richness (Figure 3).

Table 1. Direct, indirect and total standardized effect of soil nutrient and different diversity component on aboveground carbon. *p*-value in bold indicates significant effect ($p < 0.05$), based on 1000 times bootstrapping. DBH: diameter at breast height, FC: functional composition, FD: functional diversity, MCH: maximum canopy height, WD: wood density.

Predictors	Path Ways	Response	Std. Effect	95% CI		<i>p</i> -Value
				Lower	Upper	
Soil nutrient	Direct	Aboveground carbon	0.120	−0.100	0.330	0.310
Soil nutrient	Indirect effect via species richness	Aboveground carbon	0.040	−0.060	0.130	0.440
Soil nutrient	Indirect effect via FC MCH	Aboveground carbon	−0.020	−0.100	0.060	0.650
Soil nutrient	Indirect effect via DBH variation	Aboveground carbon	0.010	−0.160	0.180	0.900
Soil nutrient	Indirect effect via Functional diversity WD	Aboveground carbon	−0.010	−0.050	0.030	0.560
Soil nutrient	Indirect effect via species richness and FC MCH	Aboveground carbon	−0.020	−0.060	0.030	0.450
Soil nutrient	Indirect effect via species richness and DBH variation	Aboveground carbon	0.020	−0.030	0.060	0.480
Soil nutrient	Indirect effect via species richness and functional diversity WD	Aboveground carbon	0.000	−0.020	0.010	0.560
Soil nutrient	Sum of indirect effect	Aboveground carbon	0.010	−0.200	0.220	0.910
Soil nutrient	Total effect	Aboveground carbon	0.130	−0.170	0.420	0.400
Soil nutrient	Direct	Species richness	0.130	−0.180	0.440	0.410
Soil nutrient	Direct	FC MCH	−0.060	−0.340	0.210	0.640
Soil nutrient	Direct	DBH variation	0.020	−0.280	0.320	0.900
Soil nutrient	Direct	Functional diversity WD	0.120	−0.180	0.410	0.440
Species richness	Direct	Aboveground carbon	0.300	0.030	0.560	0.030
Species richness	Indirect effect via FC MCH	Aboveground carbon	−0.140	−0.270	0.000	0.060
Species richness	Indirect effect via DBH variation	Aboveground carbon	0.140	−0.050	0.310	0.150
Species richness	Indirect effect via functional diversity WD	Aboveground carbon	−0.040	−0.120	0.050	0.400
Species richness	Sum of indirect effect	Aboveground carbon	−0.040	−0.280	0.200	0.750
Species richness	Total effect	Aboveground carbon	0.260	−0.030	0.550	0.080
Species richness	Direct	FC MCH	−0.470	−0.740	−0.200	0.000
Species richness	Direct	DBH variation	0.230	−0.070	0.540	0.130
Species richness	Direct	Functional diversity WD	0.330	0.040	0.620	0.030
FC MCH	Direct	Aboveground carbon	0.300	0.040	0.530	0.020
DBH variation	Direct	Aboveground carbon	0.580	0.340	0.790	0.000
Functional diversity WD	Direct	Aboveground carbon	−0.110	−0.340	0.120	0.360

4. Discussion

We explored the mechanism between biodiversity (species richness, functional composition of maximum canopy height, structural diversity and functional composition of wood density) and carbon storage in the managed landscape after considering soil organic matter as a proxy for soil fertility. We found that species richness and functional composition of maximum canopy height had a positive effect on aboveground carbon storage in the structural equation model. However, both soil organic matter and species richness had no significant mediation effect on aboveground carbon storage.

4.1. Relative Importance of Biodiversity Components to Maintain Aboveground Carbon

Multiple aspects of biodiversity have been widely used in the field of ecology in recent years, to understand their relative importance in maintaining carbon storage in different forest ecosystems [1,2,14,42]. The carbon stored in forests is the result of a long-term

accumulation of plant biomass, which is generally linked to biodiversity (e.g., species, functional trait and structural) [3,7,8,14,30,40]. In our study, we included four components of biodiversity (species richness, functional diversity, functional composition and structural diversity) and hypothesized that all of them will have a positive effect on aboveground carbon storage (Hypothesis iii). We intended to explore their relative importance in Hypothesis iv. In line with our hypothesis, we found all the biodiversity components except functional diversity had a positive effect on aboveground carbon storage where structural diversity (opposing to our fourth hypothesis) posed the dominant effect compared to other three diversity components. Previous studies in different forest types have reported varying importance of these biodiversity components in the context of the study area [1–3,7,8,14,30,40]. For example, in tropical forests (the most diverse ecosystems on the earth), functional diversity plays the dominant role compared to functional composition [2]. However, in temperate and other ecosystems, such as mangrove forest and agroforestry systems with relatively lower species diversity than tropical forests, the dominant role is exerted by functional composition of plant traits or structural diversity [2,3,8,22,40,42]. Our findings in homegardens, thus revealing that in order to maximize aboveground carbon storage we need to manage stand with diverse stem size and in combination with dominant species and few other species (as species richness and functional composition of maximum canopy height also had a positive effect on aboveground carbon).

4.2. Underlying Theory of Aboveground Carbon Storage in Homegardens

Although we did not find any significant mediation effect of soil organic matter and species richness on aboveground carbon storage with hypothesis one and two (both are rejected), the findings of hypothesis three and four disclosed the underpinning mechanism of biodiversity–carbon relationship in our study area. As we found a positive effect of species richness, structural diversity (variation of DBH), functional composition of maximum canopy height on aboveground carbon storage, our study confirmed that both niche complementarity and selection effect theories are mutually inclusive in deriving aboveground carbon storage in studied homegardens. Our study also emphasized that between these two ecological theories, the niche complementarity effect theory had strong control on aboveground carbon storage in our studied homegardens. Structural diversity and species richness represent the niche complementary hypothesis, which believes that a community with diverse species ensures optimum utilization of limited resources through niche differentiation or facilitation among them [7]. While functional composition represents the selection effect theory, which assumes that carbon storage is driven by the key functional traits of the most dominant species among the diverse species in a forest stand [1,2]. Our finding is in line with a recent study on the relationship between biodiversity and aboveground carbon storage in a Sri Lankan homegarden agroforestry system, where the authors reported that structural diversity plays the dominant role in shaping the aboveground biomass [7]. However, we oppose the hypothesis that structural diversity (tree size variation), rather than species diversity determined the aboveground biomass or carbon storage in a homegarden [7,50], as we also found that species richness had a significant positive effect on aboveground carbon storage. The mutual existence of both niche complementarity effect and selection effect theories in deriving aboveground carbon storage has also been reported in other forest types. For example, a recent study in Sundarbans Reserved Forest, Bangladesh, one of the largest mangrove forests in the world, reported that the niche complementarity effect (represents by species richness) and selection effect (represented by functional composition of maximum canopy height and leaf litter nitrogen content) together enhanced carbon storage [42]. However, the dominant role was posed by the selection effect theory [42]. While in African tropical forests, Mensha et al. [2] found the dominant role of the niche complementarity effect theory over the selection effect theory in determining aboveground biomass carbon. Another study in Australian temperate forests reported that structural diversity, representing niche complementarity, suppressed the selection effect theory (represented by functional composition

of maximum canopy height and wood density) for regulating plant biomass carbon [51]. Although the above-mentioned studies (including our current study in homegardens) support the mutual existence of both theories in controlling carbon storage, the differences in the dominant role and representation of different diversity components highlight the importance of exploring biodiversity–carbon relationships in any specific study area.

Individual tree DBH variation is a forest health predictor which indicates that forest stand with high DBH variation is demographically rich, more resilient and has more niche variations compared to less structural diversity [1,7]. Diverse species in a forest stand lead to a higher stem density with varying growth forms and also provide opportunities for plant-plant mutual benefits through enhancing soil nutrients through nitrogen fixing species and thereby enhance carbon storage [2]. On the other hand, the tallest tree (representation of maximum canopy height) with a high stem DBH contains more biomass in forest and leads to a higher aboveground carbon storage at stand level [2,33]. As our findings revealed that these drivers had positive effects on aboveground carbon storage, we can conclude that homegardens with diverse species have a structurally diverse stand, favor of some dominant species and enhance carbon storage through both niche complementarity and selection effects in homegardens in a sustainable manner, similar to other types of forest ecosystems [44,52].

4.3. Limitations of This Study

We did not find any significant indirect and total effect of both soil organic matter and species richness (Figure 3; Table 1). Soil organic matter organic matter was used as a proxy of soil fertility, while for testing the mediation effect of species richness we used structural diversity, functional diversity and functional composition of wood density and maximum canopy height. However, soil nitrogen and phosphorus as a measure of soil nutrient could have direct as well as indirect effects on aboveground carbon storage in homegardens, similar to other forested ecosystems [53]. For example, it has been reported that soil phosphorus content can explain 45% of variation of aboveground carbon storage in a tropical forest in southern Costa Rica [53]. Similarly, foliar functional traits, such as specific leaf area, leaf dry matter content, leaf nitrogen and phosphorus contents, and their ratios may mediate the indirect effect of species richness on aboveground carbon storage in homegardens via functional diversity and functional composition [3,24,40,54,55]. Future research in homegarden agroforestry systems focusing on the aforementioned soil nutrients and plant foliar traits would help us better understand the biodiversity–environmental factor–carbon storage relationship.

5. Conclusions

We assessed the interaction effect of various aspects of biodiversity and soil organic matter on aboveground carbon storage in homegarden agroforestry plantations of southwestern Bangladesh. Species richness, functional composition of maximum tree height and structural diversity (variation in stand DBH) promote aboveground carbon storage. However, variation in stand DBH had a stronger influence on aboveground carbon storage than the other two components of diversity. Thus, in homegardens, both niche complementary and selection effect in combination determine aboveground carbon storage. Our findings also suggest that for maximizing carbon storage in homegardens, future plantations should carry on with site-specific dominant species, and few other species having a different growth form rather than simple monocultural practice. In this way, homegarden agroforestry systems can contribute to carbon emission reduction and adaptation targets as one of the nature-based solutions in tropical and subtropical countries.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f12121669/s1>, Table S1: Model fit statistics of all tested structural equation models in exploring biodiversity–carbon relationship, Table S2: Result of variance inflation factor test for checking multicollinearity using multiple linear regression among the covariates in the accepted structural equation model.

Author Contributions: Conceptualization, M.M.R.; methodology, M.M.R. and G.K.K.; software, M.M.R.; formal analysis, M.M.R. and G.K.K.; investigation, G.K.K. and H.A.; writing—original draft preparation, M.M.R.; writing—review and editing, M.M.R. and M.E.K.; visualization, M.M.R.; supervision, M.E.K. and M.X.; funding acquisition, G.K.K. and M.X. All authors have read and agreed to the published version of the manuscript.

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