

Co-benefits of biomass and biodiversity in a protected mountain forest of West Java, Indonesia

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Tropical mountain forests are relatively less disturbed and store a large amount of carbon in tree biomass. A high level of species diversity compared to the boreal and temperate forests is also maintained and indicates a positive relationship with tree biomass on a small scale or at plot level. This study aimed to estimate above-ground biomass stocks (AGB) and disentangle the influence of forest structure and attributes on AGB in a small mountain forest. Forty 400 m² plots were randomly established in Takokak Nature Reserve (TNR), a 60-ha protected area at an elevation between 1150-1560 m a.s.l., located in West Java, Indonesia. All trees within the plot were identified, and their respective diameter at breast height (DBH) was measured. AGB was calculated using a global allometric model. Five independent variables, *i.e.*, stem density, stem density of large trees (DBH >50 cm), community weighted mean wood density, rarefied species richness, and Fisher's alpha index, were analysed using a linear model. Our results showed that AGB in TNR was comparable to other forest types in Indonesia and acted as carbon storage in the mountain regions. AGB in the TNR reached 486 Mg ha⁻¹, of which 75% was contributed by large trees (DBH >50 cm). Three species, i.e., Liquidambar excelsa (Altingiaceae), Schima wallichii (Theaceae), and Lithocarpus sp. (Fagaceae), represent at least 70% of the total biomass in the study site. We also found that forest structures and traits, *i.e.*, stem density, stem density of large trees, and community weighted mean wood density, drive AGB variations but not tree diversity indices. However, although diversity indices were not correlated to AGB, we found that TNR is home for endemic and threatened species on the IUCN Red List. Therefore, we suggest that the management strategies of the tropical forests should include both the conservation of the carbon stock and biodiversity.

Keywords: Carbon Balance, Climate Change, Climate Mitigation, Endemic Tree, Nature Reserve REDD+, Threatened Species

Introduction

Tropical forests represent only 12% of the global land surface, but they host more than 50,000 tree species (Slik et al. 2015) and about two-thirds of the world's flowering plant species (Pimm & Joppa 2015). Trees, particularly large trees, are essential structures and often play a pivotal role in forest biomass and C dynamics (Lutz et al. 2018). They also store large quantities of carbon in the form of biomass (Slik et al. 2013, Bastin et al. 2015, Rozak et al. 2017) by sequestering carbon from the air through photosynthesis and storing it in the trunk, branches, and leaves. Trees are also crucial for soil carbon. Therefore, tropical forests are essential for carbon cycling (Le Quéré et al. 2018) and climate regulation (Bonan 2008).

The discussion of how tree diversity enhances carbon stocks in tropical forests has been a prominent research topic in recent years (Ruiz-Jaen & Potvin 2011, Poorter et al. 2015, Sullivan et al. 2017, Mensah et al. 2020). To some extent, diversity is expected to lead to facilitation and niche complementarity, increasing productivity and supporting biomass accumulation (Van

Der Sande et al. 2018). However, studies have found inconsistent results in those relationships. For instance, using Fisher's alpha metric, Sullivan et al. (2017) reported the absence of diversity-carbon relationships across tropics at a 1 ha scale. However, they detected a weak positive relationship in tropical forests of Asia, while Amazonia and Africa were absent. Another study in Neotropics reported a positive effect of rarefied species richness on AGB across 59 forest sites from Mexico to Bolivia (Poorter et al. 2015). A weak negative relationship was detected in Barro Colorado Island (Ruiz-Jaen & Potvin 2011). They reported species richness (i.e., species number) was negatively correlated with carbon storage in the natural forest but positive in the mixed-species plantation forest. These inconsistent results suggest that tree diversity-carbon relationships may depend on forest type and structure, study scale, diversity measures, and habitat heterogeneity (Ruiz-Jaen & Potvin 2011, Mensah et al. 2020).

While tree diversity-carbon relationships were inconsistent, AGB was correlated with forest structure (Lutz et al. 2018, Mensah et al. 2020), and stem density is the prominent driver of AGB (Poorter et al. 2015). Individual tree size variation typically shapes forest structure, primarily due to large trees influencing AGB (Slik et al. 2013, Bastin et al. 2015). Across the tropics, 70% of AGB variation was explained by the density of large trees (DBH >70 cm - Slik et al. 2013). Another pan-tropical study reported that large trees could predict forest structure properties related to AGB, such as mean diameter, basal area, Lorey's height, and community-weighted wood density (Bastin et al. 2018). This shows that stem density and large trees are expected to drive AGB variation, including mountain forests.

Another driver of AGB variation is functional traits. Wood density is a functional trait used as a good predictor of AGB through an allometric model (Chave et al. 2014). The value of wood density or its variation are linked to tree growth, tree mortality rates, and carbon investment (Chave et al. 2009). It correlates with morphological, mechanical, physiological, and ecological properties. Further, community-weighted wood density was found to be affected by human activities. For example, in Amazonian forests, Berenguer et al. (2014) reported that the average wood density in human-modified forests was significantly lower than in undisturbed forests, affecting their ability to store carbon in the future. Studies in the undisturbed forests, either in lowland or mountain forests in Indonesia, showed a high range value of AGB from 242 to 418 Mg ha⁻¹ (Culmsee et al. 2010, Dossa et al. 2013, Rozak & Gunawan 2015, Rozak et al. 2017), and it is also significantly higher than human-modified forests.

While the number of tropical trees carbon studies is increasing, more studies are still needed to advance our understanding of the drivers of tropical AGB, especially in a mountain forests, *i.e.*, a forest with an elevation of 1000 m a.s.l. or higher (Van Steenis et al. 1972). By far, mountain forests are less explored and still less coverage for forest carbon monitoring than other tropical lowland forests in Indonesia (Brearley et al. 2019). Several studies showed that aboveground tree biomass greatly varied across mountains (Kitayama & Aiba 2002, Rozak et al. 2017). Therefore, to predict the future global carbon balance, we need to understand the drivers of AGB variation in mountain regions, especially on a local scale. This study used data from a 60-ha protected mountain forest in Cianjur (Indonesia) to examine the influence of structural, functional, and compositional parameters on AGB. Therefore, the aims of the study were to (i) estimate AGB stocks and (ii) disentangle the influence of tree diversity, forest structure, and functional traits on AGB in a small protected mountain forest in Indonesia.

Materials and methods

Study site

We carried out the study in the mountain forest of Takokak Nature Reserve (TNR). which lies between 107° 12′ 15″ - 107° 42′ 15″ E and 07° 02' 25" - 07° 03' 06" S (Fig. 1). The forest of the TNR is estimated at ca. 60 ha and is located in Cianjur Regency, West Java, Indonesia. The minimum and maximum daily temperature reached 20 °C and 30 °C, respectively, with annual rainfall of about 4993 mm (BBKSDA Jawa Barat 2016) and classified as Af climate, which refers to a humid tropical climate with minimum annual precipitation of 60 mm yr¹ (Kottek et al. 2006). The topography of the forest consists of a rolling hilly landscape with the lowest and highest elevation of 1150 and 1560 m a.s.l., respectively. The forest hosts typical Indonesian mountain flora, e.g., Liguidambar exelsa (Altingiaceae), Castanopsis argentea (Fagaceae), Schima wallichii (Theaceae), Quercus spp. (Fagaceae), Litsea spp. (Lauraceae), and Dacrycarpus imbricatus (Podocarpaceae). Our study also found an endangered Dipterocarp species, Dipterocarpus retusus, that grows well in the forest (Ly et al. 2017). The forest is also



Fig. 1 - Map of the study site at Takokak Nature Reserve, West Java, Indonesia. The solid red line in the left panel shows the border of the nature reserve.

suitable for endemic fauna, such as Sus vitasus, Gallus gallus varius, Spilornis colaplidua, Macaca fascicularis, Trachypithecus auratus, Hylobates moloch, Presbytis comata, Spizaetus bartelsi, and Halcyon cianopentris (BBKSDA Jawa Barat 2016).

Biomass and tree height estimation

We established forty 20 \times 20 m² plots at random within the TNR, equal to 2.7% of sampling intensity. All trees with a diameter at breast height (DBH) ≥10 cm were systematically recorded, mapped, and identified to the lowest possible taxonomic level within the plots. All trees were grouped into three DBH classes, i.e., small (10-30 cm), medium (30-50 cm), and large trees (>50 cm) following classification done in the nearby mountain site by Rozak et al. (2017). Trees were identified by parabotanist, and herbarium vouchers were deposited in Herbarium Bogor Botanic Gardens. A total of 601 trees were identified at species (85.4%) and genus (14.6%) levels. Moreover, we identified about 70 tree species from 32 families (Tab. S1 in Supplementay material).

The above-ground biomass of each species (AGB_i, eqn. 1) was estimated using a generic allometric model (Chave et al. 2014). The variable used in the model were DBH (in cm), wood density (WD, in g cm 3), and tree height (H, in m). We utilised the generic allometric model because it was reported to be more accurate than the local models (Rutishauser et al. 2013). Variable WD of each species was taken from the Global Wood Density Database (Chave et al. 2009). If species were not present in the database or identified to genus level only, the genus-level average was used to estimate the wood density (Slik 2006). The tree height of each species $(H_i, eqn. 2)$ was estimated using a generic model developed for the Southeast Asia region based on DBH data (Feldpausch et al. 2012). We used a regional tree height allometric because tree DBH-height relationships differ significantly between regions, affecting AGB estimation (Feldpausch et al. 2012). Those two equations related to biomass estimation are as follows (eqn. 1, eqn. 2):

$$AGB_{i} = 0.0673 \cdot (WD_{i} \cdot DBH_{i}^{2} \cdot H_{i})^{0.976}$$
(1)
$$H_{i} = 57.122 \cdot \left[1 - \exp(1 - 0.0332 \cdot DBH_{i}^{0.8468})\right]$$

We also calculated community weighted mean wood density for each plot (CWD_i , eqn. 3) as a plant functional trait variable (Muscarella & Uriarte 2016). We weighted the wood density of each plot (WD_i) by the total basal area of each plot (BA_i); therefore, the equation is as follows (eqn. 3):

$$CWD_{j} = \sum WD_{j} \cdot BA_{j}$$
(3)

Data analysis

Linear models (eqn. 4) were developed to test the relationship between forest struc-

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ture (i.e., stem density - X₁, and stem density of trees DBH >50 cm - X_2), tree functional trait (i.e., community weighted mean wood density, CWD - X_3), and species richness indices (*i.e.*, rarefied richness, X_4 and Fisher's alpha, X₅) on above-ground biomass (AGB, Y). Two variables, AGB and Fisher's alpha, were log-transformed to fulfil the normality assumption and, therefore, minimise heteroscedasticity of residuals. We also performed a backward stepwise selection removing the nonsignificant variables from the full model (Wagner & Shimshak 2007). Since our data have varying value ranges (Tab. 1), all variables were standardised by subtracting the value by its mean and dividing it by two standard deviations of each plot (Gelman 2008). Variance Inflation Factor (VIF_i, eqn. 4) was calculated to assess the collinearity of the variables (Salmerón Gómez et al. 2016). VIF was calculated based on the coefficient of determination (R_i^2) of the linear model (eqn. 4):

$$VIF_j = \frac{1}{1 - R_j^2} \tag{4}$$

We found VIF <5 in the full model, indicating no collinearity effects (Fig. S1 in Supplementary material). The model was then inspected and validated for normality of the residuals (Fig. S2, Fig. S3). Pearson's correlation coefficients were also conducted to investigate the strength of a linear association between two variables (Lai et al. 2019). All analyses were carried on in R (R Core Team 2020), benefiting the RStudio platform. The rarefied richness and Fisher's alpha were estimated using the "vegan" package (Oksanen et al. 2017), and wood density data were collected by utilising the "BIOMASS" package (Réjou-Méchain et al. 2017) from the global wood density database (Chave et al. 2009). Data of AGB in plot level were corrected by its respective plot inclination and presented as mean with a 95% confidence interval after 1000 bootstrap replication.

Tab. 1 - All variables observed across the forty 0.04-ha plots with units, the average value, minimum value (Min), first quantile value, third quantile value, and maximum value (Max).

Variable	Unit	Average	Min	1 st quantile	3 rd quantile	Max
Biomass	Mg ha¹	486.08	32.89	264.55	579.96	1638.37
Diameter at breast height	cm	34.05	10.00	19.00	42.70	157.20
Wood density	g cm ⁻³	0.58	0.30	0.53	0.65	0.87
Stem	ha ⁻¹	247.11	19.35	149.61	338.59	469.01
Basal area	m² ha⁻¹	50.00	9.75	33.25	61.00	127.25
Rarefied richness	species	3.31	2.26	2.85	3.54	4.79
Fisher's alpha	-	14.75	2.08	5.04	13.39	117.45



Fig. 2 - Biomass variation for each diameter class. Vertical lines show their mean biomass for each diameter class, respectively.

Results

Biomass stock in Takokak Nature Reserve

Estimated AGB in the TNR reached 448 Mg ha⁻¹ (95% CI: 345-551 Mg ha⁻¹ – Fig. 2). Large trees contributed ca. 75% to the total biomass that reached 331 Mg ha⁻¹ (95% CI: 239-428 Mg ha⁻¹). Small and medium trees only contributed 10% (45 Mg ha⁻¹, 95% CI: 37-54 Mg ha⁻¹) and 16% (71 Mg ha⁻¹, 95% CI: 55-

89 Mg ha⁻¹) to the total AGB, respectively. Of those stocks, only three species, *i.e.*, *Liquidambar excelsa* (Altingiaceae), *Schima wallichii* (Theaceae), and *Lithocarpus* sp. (Fagaceae), represented 71% of the total biomass (Fig. 3).

Drivers of biomass in Takokak Nature Reserve

The explanatory variables in the full model explained 90% of the total variance of



Tab. 2 - Statistical summary of the linear model of the full model and after backward stepwise selection. (***): p<0.0001; (**): p<0.001; (*): p<0.001; (*): p<0.001;

Model	Response	Predictor	Estimate	Standard error	t-value	Pr(> t)	AICc	Adjusted R ²	p-value
Full model	AGB	Intercept	-1.59e-16	2.50e-02	0.00	1.00	-23.22	0.90	<2.2e-16
		Stem	6.54e-01	6.42e-02	10.19	7.24e-12***			
		Stem 50up	1.96e-01	7.45e-02	2.63	0.013*			
		CWD	3.07e-01	6.41e-02	4.78	3.29e-05***			
		Rarefied	-4.45e-02	5.14e-02	-0.87	0.393			
		Fisher	4.35e-02	5.40e-02	0.80	0.43			
Backward stepwise selection	AGB	Intercept	-1.55e-16	2.48e-02	0.00	1.00	-27.15	0.90	<2.2e-16
		Stem	6.74e-01	6.06e-02	11.13	3.34e-13***			
		Stem 50up	1.92e-01	7.31e-02	2.63	0.013*			
		CWD	3.01e-01	6.34e-02	4.74	3.31e-05***			





AGB (Tab. 2). Stem density, large trees, and CWD were the main drivers explaining AGB variation (Adj. $R^2 = 0.90$, p-value <0.001 – Tab. 2). We found no significant influence of rarefied richness and Fisher's alpha on the AGB full model (Tab. 2). Analysed separately, the respective diversity indices, i.e., Fisher's alpha (Adj. R² = -0.01, p-value >0.1) and rarefied richness (Adj. R² = 0.01, p-value >0.1), did not significantly explain the variation of AGB (Fig. 4). The results of the full linear model (Tab. 2) were in line with the Pearson's correlation analysis (Fig. 5). Stem density, stem density of trees DBH >50 cm, and CWD had significant effects on AGB with Pearson's coefficient values of 0.87, 0.75, and 0.60, respectively.

Discussion

Our study aims to estimate the amount of AGB stocks in a small protected lower montane forest in West Java (Indonesia), namely Takokak Nature Reserve (TNR). This study also evaluates the possible factors affecting the AGB in this area. The influencing factor will become essential information for forest managers and related stakeholders for maintaining optimum AGB within the study location in particular and Indonesian tropical montane forest in general.

Above-ground biomass in montane forests

AGB stocks in our study site reached 447 Mg ha¹ and were dominantly driven by the biomass of big trees (Fig. 2). Our estimated AGB was found to be relatively higher than other montane forests in Indonesia. In the montane forest of Central Sulawesi, AGB was estimated in the range of 301-323 Mg ha⁻¹ (Culmsee et al. 2010). While, in the montane forest of Mount Rinjani (Lombok), the AGB was estimated at 92-242 Mg ha¹ (Dossa et al. 2013). The average potential of AGB stocks in Takokak NR was also relatively higher than in the surrounding mountains of our study site. For instance, in Mount Salak (West Java), the average AGB only reached 365 Mg ha1 (Arifanti et al. 2014), and in Mount Gede Pangrango ti (West Java) reached 375 Mg ha⁻¹ (Rozak et W al. 2017). Further, AGB in our study site was st comparable to the Dipterocarp forest of th Malinau (North Kalimantan), reaching 482 Ja Mg ha⁻¹ (Rozak et al. 2018). Although these Ci comparisons might be confounded by differences in the size of plots sampled across an previous studies, our results were relatively al higher but not significantly different (to al America and Asia forests) to the estimated in at pan-tropical moist lowland forests that reached 288, 418, and 393 Mg ha⁻¹ in Neotropical, Palaeotropical, and Asia forests, tr respectively (Slik et al. 2013).

The total amount of AGB is mainly contributed from three dominant tree species, i.e., Liquidambar excelsa, Schima wallichii, and Lithocarpus sp., representing 71% of the total biomass at the plot level (Fig. 3). These three species are frequently found in mountain ecosystems in West Java Indonesia (Van Steenis et al. 1972). In our study site, those species have the highest basal area of 25.9, 20.3, and 6.99 m² ha⁻¹, respectively (Tab. S1 in Supplementary material). Those species can reach large diameters and are tall in height; consequently, they will have a large canopy where most photosynthetic carbon gain is concentrated (Poorter et al. 2015), determining their biomass (Feldpausch et al. 2012, Chave et al. 2014). This result confirms the hyper-dominant of large tree species in determining the AGB (Slik et al. 2013, Rozak et al. 2017), which is in line with other studies in investigating the influence of large trees on forest biomass (Bastin et al. 2015, Lutz et al. 2018).

The influence of forest attributes and structures on AGB in montane forest

Our analysis of the influence of tree diversitv indicates a non-statistically significant species richness-AGB relationship (Fig. 4). This result is consistent with other studies in tropical forests that also reported a lack of weak relationships (Poorter et al. 2015, Sullivan et al. 2017). However, this is true on a larger scale (plot of >1 ha - Sullivan et al. 2017). To some extent, biodiversity is expected to increase productivity through the facilitation and niche complementarity of the species. Therefore, biodiversity loss will lead to biomass loss (Cardinale et al. 2011). In our case, we worked at a small spatial scale (plot of 20 × 20 m), and we expected a positive relationship between species richness and AGB. The contrary results between other studies and ours, perhaps due to the low species richness (Tab. 1) captured within the plot caused by the dominance of a few big trees that regulate AGB in our study site (Fig. 2).

Stem densities, either small or large trees, positively drove the AGB variation (Tab. 2). Our results align with Ullah et al. (2021). The positive influence of stem density on AGB is linked with the ability of each tree to optimise resource utilisation, such as nutrients and light. It leads to higher produc-

tivity, which increases AGB (Ali et al. 2019). We found that tree density averaged 247 stem ha⁻¹ (Tab. 1) and was relatively lower than in other mountain ecosystems in West Java. For example, stem density in Mount Ciremai, Mount Gede Pangrango, and Mount Halimun Salak reached 598, 989, and 750 stem ha⁻¹, respectively (Arifanti et al. 2014, Rozak & Gunawan 2015, Rozak et al. 2017). Therefore, although stem density in our study site is relatively lower, the AGB is comparable to other ecosystems, perhaps due to the hyperdominance of large trees (Fig. 5) as found elsewhere in the tropics (Bastin et al. 2015, Lutz et al. 2018).

CWD was found to positivFig. 5ly correlate with the AGB variation (Fig. 5). This trait was related to its specific wood density and basal area: the higher the specific wood density and the larger the basal area, the higher AGB. CWD can be interpreted as physiological trade-offs related to resource availability (Muscarella & Uriarte 2016). In our case, resource availability can be defined as rapid growth due to water availability. Our study site has high annual precipitation, reaching 4993 mm yr⁻¹ (BBKSDA Jawa Barat 2016); therefore, the tree can use the resources available to grow optimally, particularly for trees with DBH >50 cm (Tab. 2). These large trees can reach the top of the canopy and maximise the sunlight for photosynthesis due to greater total leaf area (Lutz et al. 2018). Large trees also can maximise the ability of their deep root systems to absorb water and nutrient in the soil (Pinho et al. 2020). The combination of those factors then will ultimately lead to higher productivity and AGB.

Biomass and biodiversity conservation in montane forest

Assessing the relationships between tree species richness and AGB is crucial for the effective management of the tropical forest, such as carbon sequestration and biodiversity conservation within the Reducing Emissions from Deforestation and forest Degradation (REDD+) framework scheme (Enrici & Hubacek 2018). Although species richness indices were not significantly related to AGB (Tab. 2), it consists of important species for conservation. In our study site, several recorded species composing the montane flora (the complete list of the species is available in Tab. S1) are known to be endemic to Java (e.g., Pinanga javana, Arecaceae) and categorised as Threatened species by IUCN Red List, such as Dipterocarpus retusus, Dipterocarpaceae (Endangered, EN), Castanopsis tungurrut, Fagaceae (Endangered, EN), and Lithocarpus indutus, Fagaceae (Vulnerable, VU) (IUCN 2021). These species are an important component of montane forests in Java and have significant conservation value as flagship species for promoting biodiversity conservation. Considering that TNR is a relict montane forest in West Java, apart from Mount Gede Pangrango and Mount Halimun Salak, the populations of these species could contain valuable genetic resources for future conservation programs such as population enhancement or reintroduction as well as habitat restoration. The forest area in Java has been severely affected by deforestation and degradation. West Java, where the TNR was located, had lost around 40% of its montane forest since 1990 (Higginbottom et al. 2019). Therefore, TNR has a significant value in carbon storage and biodiversity conservation for endemic and threatened tree species under these circumstances and could be classified as Important Plants Areas (IPA) in the tropics (Darbyshire et al. 2017).

Conclusion

Carbon balance in the tropical mountain forest of Indonesia

Our study provided an AGB estimation in a mountain rainforest and disentangled the effect of forest structures and attributes on AGB. We found that the AGB in TNR was comparable to other forest types in Indonesia. We also found that three variables, *i.e.*, stem density, stem density of large trees, and community weighted mean wood density, drive AGB variation. Further, no correlation was found between AGB and species diversity indices, indicating a neutral influence of biodiversity on carbon balance in the forests. However, our study site was diverse in tree diversity and it is home to several endemic and threatened trees listed in IUCN Red List. Therefore, conservation strategies of mountain forests should be applied simultaneously between carbon-centred- and biodiversityconservations.

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AHR, YWCK, and DIJ contribute equally to this work as the main contributor. AHR, YWCK, and DIJ designed the project, conducted fieldwork, and performed the analysis. AHR wrote the first draft of the manuscript. AHR, YWCK, and DIJ wrote, revised, and approved the manuscript.

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Supplementary Material

Fig. S1 - Variance inflation factors among variables used in the full model.

Fig. S2 - Nonnormality of residuals between theoretical quantiles and studentized residuals of the full model.

Fig. S3 - Distribution of residuals of the full model.

Tab. S1 - Species, family, basal area (m²), cumulative basal area (m²), above-ground biomass (Mg), cumulative above-ground biomass (Mg) for each species found in Takokak NR, West Java, Indonesia.

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