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Demography, Structure, and Composition of a Low-Disturbance Forest in Luzon, Philippines

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ABSTRACT

Tropical forests continue to face deforestation in countries such as the Philippines. To look at the long-term behavior of forests in response to intrinsic and extrinsic factors, continual monitoring of forest dynamics is needed. To do this, we established a 2-ha permanent tropical forest plot in a low-disturbance area in Maluyon, Philippines. We addressed three main questions: 1) How does the plot change through time? 2) How do different species in the plot change through time? 3) Would the responses differ by tree size? We measured, mapped, and identified all trees $\geq$1 cm in diameter in 2011. In 2015, we re-measured surviving trees and measured, mapped, and identified recruits. A total of 177 tree species were found in the plot. The forest exhibited a mean growth rate of 0.054 cm/year, mortality rate of 0.011%/year, and recruitment rate of 0.019%/year. Overall growth and mortality rates were lower in Maluyon than in other plots, possibly due to the forest's high tree density and low disturbance. Species-specific rates revealed the presence of both the growth-survival and the stature-recruitment trade-offs. Size class analysis showed higher growth rates in large-sized than in small-sized trees. In contrast, small-sized trees exhibited a higher mortality rate compared to large-sized trees, likely due to density dependence. Key findings of the study may be utilized to increase the success rate of restoration efforts in this watershed. Using a mix of fast-growing, generalist species with high survival rates (e.g., *Allophyllus cobbe* and *Anisoptera thurifera*) is highly recommended.

1. INTRODUCTION

Tropical forests are among the largest reservoirs of the world's biodiversity, supporting roughly 60% of the Earth's total species (Andresen et al., 2018; Handley, 2018). They have the highest gross primary productivity out of all the terrestrial biomes and account for one-fourth of terrestrial carbon (Beer et al., 2010; Pinmongkhonkul et al., 2023). Across different regions, forest structures vary depending on the biotic and abiotic forces they are exposed to (Davies et al., 2021). These environmental stresses impact forest growth and productivity, mortality, and species demographics (McDowell et al., 2020). As such, continual monitoring of forest dynamics provides much-needed information on the long-term behavior of forests (Davies et al., 2021).

In the Philippines, tropical forest ecosystems have drastically reduced over time. Early reports show that, in 1934, the country had roughly 17 million hectares worth of forest vegetation (Bautista, 1990). However, from 1980 to 1987, deforestation in the Philippines averaged approximately 157,000 hectares per year, with illegal operations persisting into the 21st century (Kummer, 1992; Lopez, 2020). In addition, the Philippines ranks first worldwide for countries with the highest disaster risk index due to frequent tropical cyclones (Atwii et al., 2022). As of 2015, available forest cover had reduced to 7 million

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hectares, constituting a sharp, 59% decrease in less than a century (Forest Management Bureau, 2018).

Combining the expanding threat of land conversion and the increase of stronger typhoons, it is predicted that these environmental stresses affecting the country's remaining forest ecosystems would only worsen over time (Yih et al., 1991). This entails the need to conduct extensive studies to examine long-term distributional patterns of Philippine tropical forests.

Despite the clear importance of tropical forests and their alarming vulnerability in the country, Philippine forests remain biologically under-surveyed to this day (Pang et al., 2021). In-depth studies of Philippine forest responses are limited, with a majority of these sites surveyed following major anthropogenic or natural disturbances. For example, regenerating forest sites were studied in Leyte Island to determine the impact of major slash-and-burn farming (known locally as *kaingin*) on forest composition and structure (Mukul et al., 2020). Another forest dynamics plot in the Philippines, the Palanan Forest Dynamics Plot in Isabela, Luzon island was monitored following its exposure to typhoons (Pasion et al., 2022; Yap et al., 2016). These studies show that major disturbances indeed pose a heavy influence on forest structure. But what happens in these forests when there are no major disturbances? Studies on Philippine forests with little to no disturbances are needed to characterize the baseline dynamics in intact rainforests. Thus, we established the Maluyon Permanent Forest Dynamics Plot, a low-disturbance plot located in Nueva Ecija, Luzon Island, Philippines. Characterized as an uneven-aged forest with mountainous terrain, the area has a monthly temperature range of 23.21°C to 31.1°C, an average annual relative humidity of 83.37%, and an annual average rainfall of 176.65 cm (Lasco et al., 2010).

Three major questions were addressed in the study: (1) How does the plot change through time?, (2) How do the populations of different species in the plot change through time?, and (3) Would the changes differ by tree size?

The study first analyzed plot-level changes in community-weighted functional traits (e.g., species abundance and basal area) and demographic rates. Secondly, the demographic rates of each species were evaluated by determining their corresponding recruitment rate, growth rate, and mortality rate during the 4-year interval between the 2011 and 2015 forest censuses. The plot's overall forest dynamics were then assessed using demographic rates per size class.

Corresponding findings from the study were used to discuss whether these demographic shifts are also manifested by forests across the globe. This opens up another emerging field of interest covered by forest dynamics, which is the generation of models for predicting forest behavior. These generalized models would be able to curate pre-determined inferences of changes in the functional composition and structure of forests in response to periodic, environmental stresses - thereby enforcing optimized interventions in response to timely environmental issues such as deforestation and climate change.

In summary, the study was able to generate (1) plot-level forest changes, (2) demographic rates for all species found in the plot, and (3) demographic changes per size class.

2. METHODOLOGY

2.1 Plot establishment and monitoring

The Maluyon Permanent Forest Dynamics Plot (MPFDP) is a 2-ha lowland tropical rainforest plot located in Mt. Maluyon of the Pantabangan-Carranglan Watershed Forest Reserve in Pantabangan, Nueva Ecija, Luzon island, Philippines (15°52'25.25''N, 121°03'32.75''E, Figure 1). The plot was established in 2011 as part of the Biodiversity Conservation and Monitoring Program of the First Gen Hydro Power Corporation. Following the ForestGEO Network's protocol (Condit, 1998), all free-standing stems ≥1 cm diameter at breast height (DBH) within the plot were measured, tagged, mapped, and identified to species- (or morphospecies-) level. Individuals whose complete scientific names were not known were assigned unique descriptors instead. Site mapping was conducted by dividing the plot into 20×20 m^2 quadrats with 5×5 m^2 sub-quadrats each. The corresponding x-y coordinates of each individual tree were then obtained through in situ mapping.

The MPFDP was then re-censused in 2015. All surviving stems were measured at their original points of measurement. All new stems ≥1 cm diameter at breast height (DBH) (termed as recruits) were measured, tagged, mapped, and identified to species- (or morphospecies-) level.

The study area has high tree endemicity at 61%, among which 28% of the species were classified as rare. The presence of anthropogenic disturbances in the watershed, such as illegal logging, slash-and-burn farming, and livestock grazing - all of which were performed solely by locals - had also been previously documented (Pabico et al., 2021). As of 2011, there have been no anecdotes or documentation that the MPFDP has been impacted by typhoons or other natural disturbances.

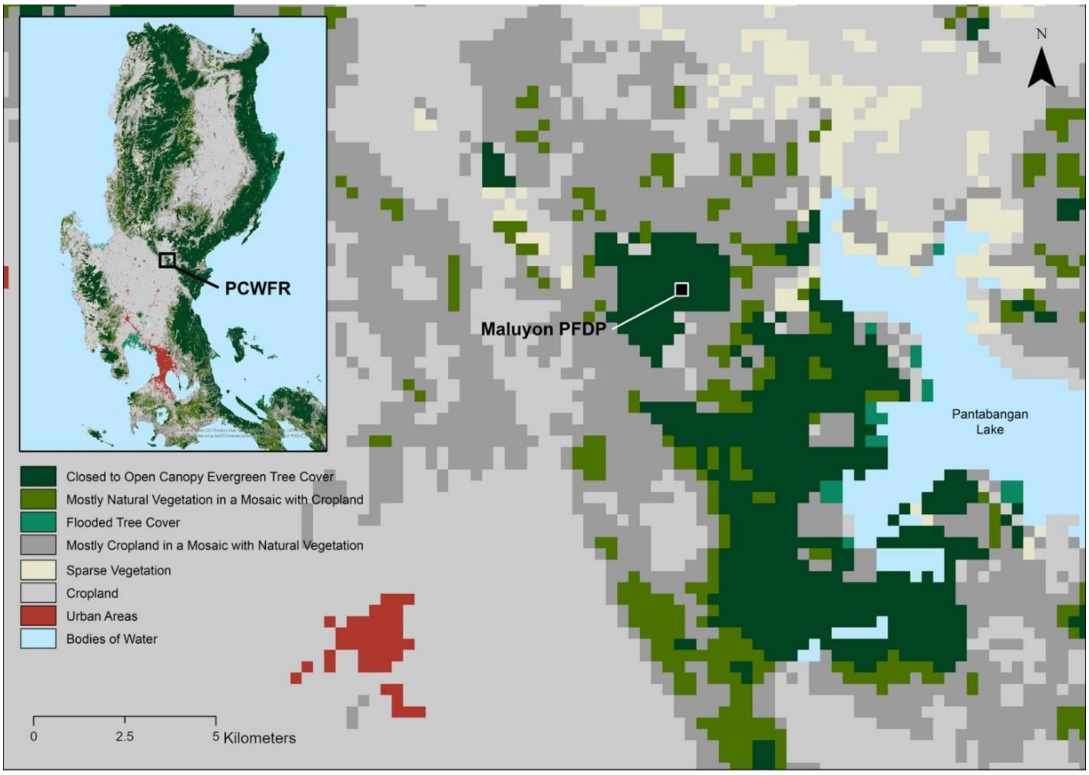

Figure 1. Location map of the Maluyon Permanent Forest Dynamics Plot (PFDP), established in 2011 inside the Pantabangan-Carranglan Watershed Forest Reserve (PCWFR), Nueva Ecija, Philippines. Inset: Luzon Island, Philippines.

2.2 Data management

Each tree individual entry logged into the database should have met the specified criteria. Only the main stem was used for data analysis because abundance, frequency, and demographic rates are based on individual tree data and also because we did not estimate aboveground biomass in this study.

Datasets were loaded into R, which served as the main software for data management and code execution (R Core Team, 2020). Tables for the 2011 and 2015 censuses were cleaned to ensure that the following data conditions were met: (1) each entry must be tagged as either alive (A), dead (D), or a recruit (" " in 2011, "A" in 2015) and (2) both datasets contained the same number of entries. Duplicates were further identified based on the uniqueness of each individual's stem ID, and these were either manually deleted or tagged with a new unique stem ID.

2.3 Species abundance, basal area, and importance value

The study utilized the *fgeo* R package for data analysis and transformation (Lepore et al., 2019). Three traits were analyzed per species: 1) species abundance, defined as the count of individuals for each unique species; 2) relative abundance, defined as the proportion of species abundance to the total number of sampled individuals; and 3) basal area, defined as the area occupied by trees at breast height.

We also computed the Importance Value Index (IVI), originally described by Curtis and McIntosh (1951) as the relative importance of a tree species within a stand. It is computed by summing up three separate values per tree species: relative frequency ((number of subplots where a species is present/50 subplots) × 100%), relative abundance ((number of individual trees of a species/total number of individuals in the plot) × 100%), and relative density ((total basal area of a species/total basal area in the plot) × 100%). A tree species can have a maximum IVI value of 300 and more important species in the stand have higher IVI values (Curtis and McIntosh, 1951).

2.4 Demographic rates analysis

Forest dynamics patterns were analyzed by determining demographic rate changes in the 2-hectare MPFDP through the 4-year time interval of the two censuses. Trees were first grouped per species. The growth, recruitment, and mortality rates were then calculated using the *fgeo* R package, whose corresponding equations for the demographic rates are as follows:

$$\text{Growth Rate} = \frac{\text{DBH}_{2015} - \text{DBH}_{2011}}{\text{T}}$$

$$\text{Mortality Rate} = \frac{\log[\text{N}_{2011}] - \log[\text{N}_\text{S}]}{\text{T}}$$

$$\text{Recruitment Rate} = \frac{\log[\text{N}_{2015}] - \log[\text{N}_\text{S}]}{\text{T}}$$

Where; DBH_{2015}=diameter at breast height measured in 2015 (in cm), DBH_{2011}=diameter at breast height measured in 2011 (in cm), T=time interval between censuses (in years), N_{2011}=total number of individual trees in 2011, N_{2015}=total number of individual trees in 2015, and N_S=total number of surviving individual trees in 2015.

To determine if tree size would affect tree response, demographic rates were also computed based on the following size class categories: (1) small (1≤DBH≤10 cm); (2) medium (10 cm<DBH≤20 cm); and (3) large (DBH>20 cm).

3. RESULTS

3.1 Forest composition and plot-level dynamics

Overall, a total of 177 tree species were recorded in the 2-ha Maluyon Permanent Forest Dynamics Plot (MPFDP), belonging to 91 families and 97 genera. An initial tree community of 175 tree species was censused in 2011. However, this was reduced to 172 species by 2015. Five species from the 2011 census were not documented again in the next census (Table S1). However, two additional species were seen in 2015 (*Artocarpus blancoi* and *Canthium* sp. 1). Tree abundance increased from 10,658 tree individuals in 2011 to 10,686 recorded individuals in 2015 (accounting for 572 recruits and 544 tree deaths). The increase in tree abundance also led to an increase in tree density (Table 1). Tree density increased from 4,824 individuals per hectare in 2011 to 5,343 individuals per hectare in 2015.

The most abundant species in the plot were similar in 2011 and 2015 (Table S2). Species-specific basal areas also showed little change in both census years (Tables S3 and S4). *Camellia lanceolata* (Theaceae) was the most dominant tree species constituting 18.95% of all individuals in the initial census, and having the highest IVI (Table 2). Despite being only half as abundant as *C. lanceolata*, *Mangifera monandra* had the highest basal area totaling 29.82% of the basal area of the whole plot, and the second-highest IVI (Table 2).

Trees inside the plot showed an overall mean growth rate of 0.054 cm/year, a mean mortality rate of 0.011%/year, and a mean recruitment rate of 0.019%/year (Table 1).

Table 1. Forest demography in the Maluyon Permanent Forest Dynamics Plot

Census year	Tree density (individuals/ha)	Growth (cm/year)	Mortality (%/year)	Recruitment (%/year)
2011	4,824	0.054	0.011	0.019
2015	5,343			

3.2 Species-level demography

Demographic rates varied across species. A species from the genus *Aglaia* exhibited the highest increase in girth, with a growth rate of 0.650±2.69 cm/year (Table 3). Five other species grew at least 0.2 cm/year (Table 3; *Elaeocarpus* sp. 01, *Lithocarpus* sp. 04, *Syzygium* sp. 10, *Ficus* sp., and *Palaquium heterosepalum*). On the other side of the growth spectrum, many species had no growth. Of the species that were represented by more than one individual, five species, *Ardisia philippinesis* (n=25), *Artocarpus* sp. 02, *Celtis luzonica*, *Leucosyke capitellata*, and *Mitrephora* sp. 02 did not grow in diameter during the 4-year study period (Table 4).

The annualized mean mortality rate in the plot was low. Among species, an unidentified species had the highest mortality rate was 0.173%/year (Confidence Interval (CI): 0.025-0.590%/year) (Table 5). This was followed by *Claoxylon* sp. and *Calophyllum soulattri*, *Ficus congesta*, and *Sterculia ceramica* with a mean mortality rate of 0.101%/year. It was further observed that a total of 96 species had a mortality rate of 0 (Table S6). Among these, 81 species had populations of ≤10 individuals.

Table 2. Most abundant species in the Maluyon Permanent Forest Dynamics Plot in 2011. Species included in this table are those with more than 100 individuals/ha. DBH stands for diameter at breast height.

Species	Family	Relative abundance (%)	Basal area (cm^2)	Density (individuals/ha)	Maximum DBH (cm)	Mean DBH (cm)	Importance value index (IVI)
Camellia lanceolata	Theaceae	18.95%	33,900	1,010	18.4	3.91	20.99
Mangifera monandra	Anacardiaceae	9.00	230,600	480	65.6	11.77	11.30
Cinnamomum mercadoi	Lauraceae	7.89	40,600	421	30.2	5.81	9.94
Allophyllus cobbe	Sapindaceae	3.70	46,500	197	54.3	7.65	5.60
Garcinia rubra	Clusiaceae	3.54	3,080	189	10.6	2.68	5.54
Anisoptera thurifera	Dipterocarpaceae	3.26	48,700	174	81.9	8.42	5.32
Syzygium sp. 02	Myrtaceae	2.77	47,800	148	34.6	11.00	4.07
Atalantia racemosa	Rutaceae	2.64	3,170	141	12.2	3.14	4.52
Syzygium sp. 01	Myrtaceae	2.24	10,900	120	31.5	5.48	3.13
Palaquium bataanense	Sapotaceae	2.19	13,300	117	40.7	6.13	4.12
Memecylon sorsogonense	Melastomataceae	2.15	670	115	5.2	1.81	4.15
Aporosa symplocifolia	Phyllanthaceae	1.93	5,920	103	14.2	5.18	3.46
Other species (n=163)		39.74	76,835,060	5,490			

As to recruitment rate, a species of *Celastrus* exhibited the highest annualized mean rate (0.275%year, CI: 0.054-0.674%/year), followed by *Garcinia* sp. 03, *Aglaia elliptica*, *Artocarpus* sp., *Heritiera sylvatica*, *Dysoxylum excelsum*, *Garcinia* sp. 04, and *Leucosyke capitellata* (Table 6). On the other hand, a total of 88 species in the plot had a recruitment rate of 0%/year (Table S7).

3.3 Variation in demographic rates according to size class

Large-sized trees had the highest growth rates (0.154±0.023 cm/year), followed by medium-sized (0.079±0.008 cm/year), and then small-sized trees (0.035±0.003 cm/year) (Figure 2). In terms of mortality, small-sized trees in the plot had the highest mortality rate among the size classes (0.014%/year), followed by medium-sized (0.009%/year) and large-sized trees (0.005%/year). The mortality rate of small-sized trees was significantly different from the other two. The annualized mean recruitment rate inside the plot was 0%/year for all size classes.

Table 3. Tree species with the highest growth rates in the Maluyon Permanent Forest Dynamics Plot. N=number of individual trees

Rank	Species	N	Rate (cm/year) ±95% confidence interval
1	*Aglaia* sp. 05	2	0.650±2.69
2	*Elaeocarpus* sp. 01	4	0.538±0.485
3	*Lithocarpus* sp. 04	10	0.373±0.235
4	*Syzygium* sp. 10	1	0.250
5	*Ficus* sp.	2	0.21±0.91
6	*Palaquium heterosepalum*	4	0.2±0.3
7	*Syzygium densinervium*	73	0.177±0.259
8	*Artocarpus ovatus*	1	0.175
9	*Ficus* sp. 05	1	0.175
10	*Chionanthus* sp. 01	4	0.156±0.203
11	*Artocarpus* sp.	1	0.150
12	*Astronia williamsii*	12	0.14±0.11
13	*Terminalia macrantha*	62	0.14±0.061
14	*Radermachera pinnata*	5	0.14±0.20
15	*Allophyllus cobbe*	381	0.13±0.017
16	*Elaeocarpus* sp.	41	0.112±0.101
17	*Actinodaphne ramosii*	25	0.111±0.063
18	*Shorea guiso*	44	0.11±0.05
19	*Ficus variegata*	3	0.108±0.345
20	*Maranthes corymbosa*	69	0.108±0.039

Table 4. Tree species with the lowest growth rates in the Maluyon Permanent Forest Dynamics Plot. Species with 0% mortality rates are indicated with an (*).

Rank	Species	N	Rate (cm/year) ±95% confidence interval
1	*Aglaia* sp. 03*	1	0
2	*Alstonia scholaris**	1	0
3	*Artocarpus* sp. 02*	2	0
4	*Celastrus* sp. 02*	1	0
5	*Celtis luzonica**	2	0
6	*Dysoxylum* sp. 04*	1	0
7	*Monoon* cf. *klemmei*	6	0±0.088
8	*Ficus congesta*	1	0
9	*Ficus carpenteriana**	1	0
10	*Leucosyke capitellata**	2	0
11	*Melicope* sp. 01*	1	0
12	*Mitrephora* sp. 02	4	0

Table 4. Tree species with the lowest growth rates in the Maluyon Permanent Forest Dynamics Plot. Species with 0% mortality rates are indicated with an (*) (cont.).

Rank	Species	N	Rate (cm/year) ±95% confidence interval
13	*Palaquium* cf. *lanceolatum**	1	0±0.186
14	*Ardisia philippinensis*	25	0
15	*Glochidion luzonense*	17	0.004±0.028
16	*Symplocos* sp. 03	22	0.004±0.013
17	*Clausena anisum-olens*	4	0.005±0.008
18	*Antidesma* sp.	11	0.006±0.017
19	*Glycosmis* cf. *parviflora*	18	0.007±0.015
20	*Ficus pseudopalma**	3	0.007±0.031

Table 5. Tree species with the highest mortality rates in the Maluyon Permanent Forest Dynamics Plot. N=number of individual trees; D=number of deaths

Rank	Species	N_{2011}	D_{2015}	Annualized mean Rate (%/year)	Confidence interval	
					Lower	Upper
1	Unidentified species 09	2	1	0.173	0.025	0.590
2	*Claoxylon* sp.	12	4	0.101	0.037	0.238
3	*Calophyllum soulattri*	3	1	0.101	0.017	0.410
4	*Ficus congesta*	3	1	0.101	0.017	0.410
5	*Sterculia ceramica*	3	1	0.101	0.017	0.410
6	*Memecylon lanceolatum*	12	3	0.072	0.024	0.193
7	*Shorea astylosa*	9	2	0.063	0.017	0.203
8	*Mitrephora* sp. 02	5	1	0.056	0.011	0.256
9	*Ardisia pyramidalis*	128	24	0.052	0.035	0.077
10	*Dysoxylum* sp. 02	6	1	0.046	0.009	0.216
11	*Guioa discolor*	64	10	0.042	0.023	0.077
12	*Syzygium* sp. 02	295	43	0.039	0.029	0.053
13	*Glycosmis* cf. *parviflora*	21	3	0.039	0.013	0.107
14	*Microcos stylocarpa*	7	1	0.039	0.008	0.187
15	*Prunus marsupialis*	14	2	0.039	0.011	0.130
16	*Calophyllum* sp.	159	22	0.037	0.025	0.056
17	*Aglaia edulis*	23	3	0.035	0.012	0.098
18	*Archidendron clypearia*	55	7	0.034	0.016	0.069
19	*Lithocarpus* cf. *philippinensis*	119	14	0.031	0.019	0.052
20	*Lithocarpus* sp.	34	4	0.031	0.012	0.078

Table 6. Tree species with the highest recruitment rates in the Maluyon Permanent Forest Dynamics Plot. N=number of individual trees; R=number of recruits

Rank	Species	N_{2015}	R_{2015}	Annualized Mean Rate (%/year)	Confidence Interval	
					Lower	Upper
1	*Celastrus* sp. 02	3	2	0.275	0.054	0.674
2	*Garcinia* sp. 03	5	3	0.229	0.063	0.534
3	*Aglaia elliptica*	2	1	0.173	0.025	0.590
4	*Artocarpus* sp.	2	1	0.173	0.025	0.590
5	*Heritiera sylvatica*	2	1	0.173	0.025	0.590
6	*Dysoxylum excelsum*	2	1	0.173	0.025	0.590
7	*Garcinia* sp. 04	2	1	0.173	0.025	0.590
8	*Leucosyke capitellata*	4	2	0.173	0.040	0.480
9	*Calophyllum soulattri*	3	1	0.101	0.017	0.410

Table 6. Tree species with the highest recruitment rates in the Maluyon Permanent Forest Dynamics Plot. N=number of individual trees; R=number of recruits (cont.)

Rank	Species	N_{2015}	R_{2015}	Annualized mean rate (%/year)	Confidence interval	
					Lower	Upper
10	*Croton* sp. 01	3	1	0.101	0.017	0.410
11	*Elaeocarpus* sp. 01	6	2	0.101	0.026	0.309
12	*Calophyllum blancoi*	7	2	0.084	0.022	0.263
13	*Symplocos* sp. 03	30	8	0.078	0.038	0.148
14	*Mitrephora* sp. 02	5	1	0.056	0.011	0.256
15	*Champeria manillana*	61	12	0.055	0.031	0.094
16	*Chionanthus* sp. 02	11	2	0.050	0.014	0.165
17	*Memecylon lanceolatum*	11	2	0.050	0.014	0.165
18	*Tarrenoidea wallichii*	6	1	0.046	0.009	0.216
19	*Psychotria* sp. 01	32	5	0.042	0.018	0.096
20	*Sterculia comosa*	27	4	0.040	0.016	0.099

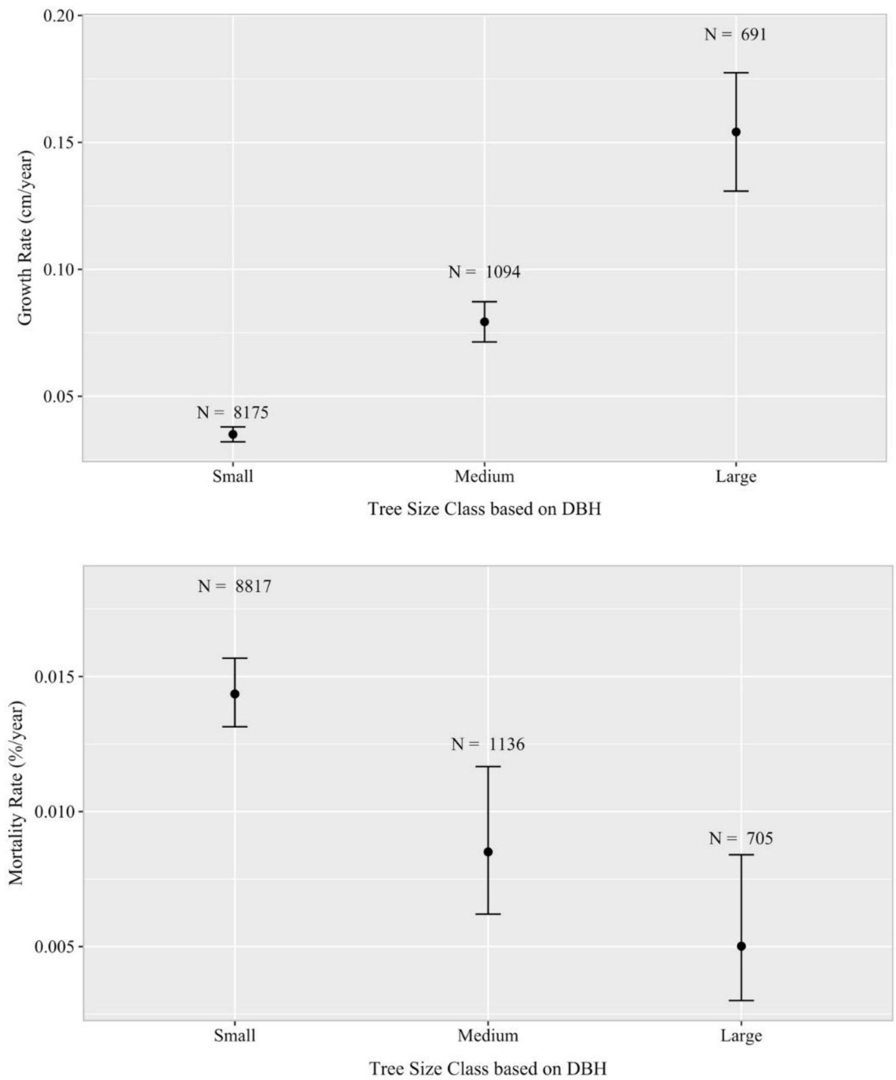

Figure 2. Demographic rates of tree individuals in the Maluyon Permanent Forest Dynamics Plot grouped per size class.

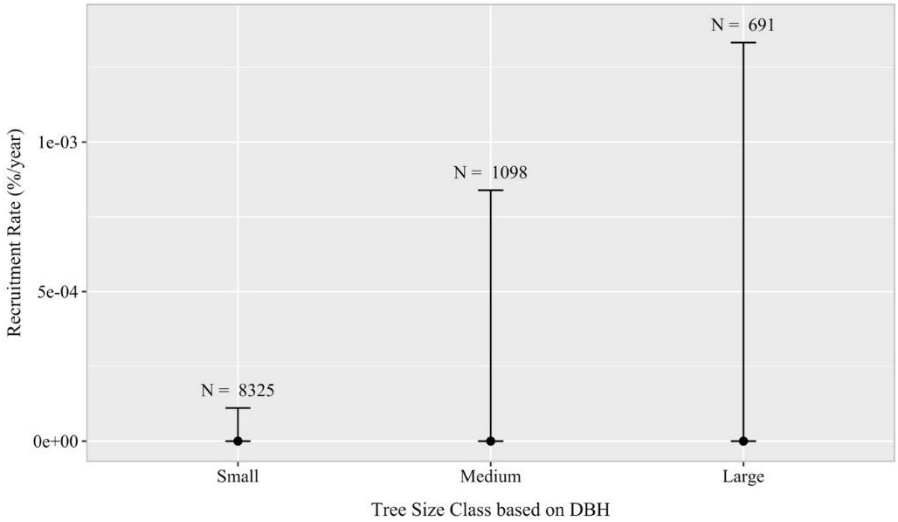

Figure 2. Demographic rates of tree individuals in the Maluyon Permanent Forest Dynamics Plot grouped per size class (cont.).

4. DISCUSSION

Forest dynamics provide a crucial understanding of how ecosystems behave with the changing climate. The response of forest communities to external and interspecific pressures provides vital knowledge on forest resiliency and possible adaptations amid these disturbances (Thompson et al., 2009). Here, a detailed discussion on the changes in plot-, species-, and stature-level responses in the Maluyon Permanent Forest Dynamics Plot (MPFDP) over 4 years is presented.

4.1 Plot-level demography

Forest dynamics is primarily described using three demographic rates: growth, mortality, and recruitment rates. Growth in the Maluyon plot was observed to be much slower in comparison to that of typhoon-prone forests. The Luquillo Plot in Puerto Rico and the Fushan Plot in Taiwan, for example, both exhibited growth rates greater than 0.10 cm/year (Hogan et al., 2018). This was also the case for the Palanan Plot in the Philippines, which exhibited even higher growth rates (0.117-0.164 cm/year) (Hogan et al., 2018). These rates are more than twice the average growth rate in Maluyon (Table 1). Across existing permanent forest plots, the Maluyon growth rate was instead closest to that of the Barro Colorado Island (BCI) forest in Panama during some census intervals, where the BCI forest exhibited growth rates of 0.025-0.080 cm/year (Hogan et al., 2018). Like the Maluyon Plot, the BCI forest is a tropical forest with no recorded strong tropical cyclones directly affecting it. Apart from the lack of tropical cyclones in the Maluyon area, the slower growth may be associated with increased competition brought about by higher tree density. Across different tropical forests, tree growth was negatively affected by neighborhood crowding (Rozendaal et al., 2020). In 2015, tree density in the Maluyon Plot was 5,343 trees per hectare, whereas Palanan tree density in 2010 was 4,708 trees per hectare (Yap et al., 2016). Maluyon's tree density is also higher than that of the Luquillo Plot in 2016, which was 1,857 trees per hectare (Zimmerman, 2020). Higher tree density may lead to higher competition for resources in the Maluyon Plot, which may have led to its relatively slow growth rate.

As to mortality rate, the Maluyon Plot had a lower mean rate (0.011%/year) compared to the Palanan Plot (2.05±0.03%/year) (Yap et al., 2016; Hogan et al., 2018). Mortality rate in Maluyon was lower than that of other forests as well, such as the Kolombangara forest in the Solomon Islands (1.4-2.2%/year) and the CTFS-ForestGEO large forest dynamics plot in Virginia, USA (1.4-2.1%/year) (Gonzalez-Akre et al., 2016). This lower mortality in the Maluyon Plot in contrast to that of other forests may also be due to the lack of disturbances (Hogan et al., 2018). Lastly, recruitment rate in the Maluyon Plot (0.019%/year) was similar to the recruitment rates of other Asia-based plots during typhoon-free intervals. Particularly, recruitment rate was most similar to the Luquillo Plot (0.014-0.092%/year) and the Palanan Plot (0.016%/year) in periods where no typhoons were observed.

Overall, the presence of periodic, high-intensity forest disturbances seems to play a significant role in driving demographic rates among these forests. Moreover, similarities in climate seasonality, biogeography, and geology may have a less significant role in shaping forest dynamics (Russo et al., 2021). This is clearly illustrated in the Maluyon and Palanan Plots, which are both located in Luzon Island, Philippines. The growth rate in Palanan is more than twice that of Maluyon, but their mortality and recruitment rates are similar during Palanan's non-typhoon interval. Nonetheless, there remains much opportunity to further investigate the broad set of factors that contribute to tree growth and survival, such as microclimate variations, functional trait shifts, and interspecific interactions (Monoy et al., 2016; De Frenne et al., 2021; Detto et al., 2022).

4.2 Species-level demography

Globally, tropical forest communities are largely structured according to two demographic trade-offs: (1) the growth-survival trade-off and (2) the stature-recruitment trade-off (Rüger et al., 2020; Russo et al., 2021; Kambach et al., 2022). These trade-offs postulate that plants can allocate their limited resources to (1) either fast growth or long survival and (2) either tall stature or increased recruitment. Combining these two trade-offs, Rüger et al. (2020) categorized species into five functional groups: Slow, Fast, Long-lived pioneer, Short-lived breeder, and Intermediate. Given the resulting species-specific demographic rates, these two trade-offs were evident in the Maluyon Plot.

At the extreme end of the growth-survival spectrum, there are "Slow" species in the Maluyon Plot that have the lowest growth rates and the highest survival rates (i.e., 0% mortality) (Tables 4 and S6). Eleven out of the 20 species in Table 4 have 0% mortality. These include *Ficus pseudopalma*, *Palaquium* cf. *lanceolatum*, *Leucosyke capitellata, and Celtis luzonica*. Three species in the Maluyon Plot are at the other end of this growth-survival spectrum. These are the "Fast" growers, with the highest mortality rates: *Archidendron clyperia* (growth rate: 0.078 cm/year, rank 18th in mortality), *Guoia discolor* (growth rate: 0.077 cm/year, rank 11th in mortality), and *Shorea astylosa* (growth rate: 0.071 cm/year, rank 7th in mortality).

Short-lived breeders are also well-represented in the Maluyon Plot. These are the species that attain low tree stature but compensate with high levels of recruitment (Rüger et al., 2020). Three species best represent this group in the plot: *Camellia lanceolata*, *Celastrus* sp. 02, and *Garcinia* sp. 03. The most abundant tree in the plot is *C. lanceolata* and it had an additional 96 recruits in 2015. However, it only has a mid-range tree stature (maximum DBH: 18.40 cm). Its abundance is possibly linked to its ability to fruit and flower in the Philippines almost all year round (Galindon, *pers. obs.*). *Celastrus* sp. 02 had the highest recruitment rate but one of the lowest maximum DBH (1.7 cm). Similarly, *Garcinia* sp. 03 had the second-highest recruitment rate but one of the lowest maximum DBH (2.0 cm).

Like in the Maluyon Plot, the growth-survival and stature-recruitment trade-offs are also observed in the Palanan Plot, despite it being a disturbance-prone forest (Russo et al., 2021; Kambach et al., 2022). The establishment and monitoring of additional plots in other Philippine islands will give us a further understanding of the generality of these trade-offs in shaping Philippine forest diversity.

4.3 Variation in demographic rates according to size class

It was demonstrated that as tree size increased, growth rates increased, while mortality rates decreased. This pattern was also the case for the Mudumalai forest in India, where large-sized trees had the lowest mortality rates and small-sized trees exhibited the highest growth rates (Sukumar et al., 2004). Mortality rates across forests are said to be density-dependent, and further driven by the direct and indirect effects of anthropogenic perturbations (Lutz et al., 2014; Anderson-Teixeira et al., 2015). We see this in the MPFDP where small-sized trees had the highest size class population and the highest mortality rate. Conversely, large-sized trees had the lowest size class population, which may explain why they exhibited lower mortality.

Recruitment rate inside the plot was observed to be 0%/year for all size classes, thus suggesting a slow recruitment rate for the entire area. Particularly, small-sized trees had the lowest recruitment rate of the three size classes. This may be attributed to the overshadowing of tall, mature trees with large canopies, therefore limiting the availability of light for growth (Coomes and Allen, 2007).

4.4 Implications to forest conservation and restoration

The Maluyon Plot is an integral part of the Pantabangan-Carranglan Watershed Forest Reserve. It is an important conservation area because threatened forest species, such as *Shorea contorta* (Dipterocarpaceae) and *Palaquium bataanense*

(Sapotaceae), which are both included in the IUCN Red List of Threatened Species, are abundant inside the plot.

The extensive data from the plot can also be used to craft science-based forest restoration efforts because it is important to look into species characteristics, such as their survival rate and distribution, to evaluate their effectiveness in forest rehabilitation (Marod et al., 2022). Species to be selected for restoration programs should be native, representative of the flora in the area, and able to accelerate ecological succession (Elliott et al., 2022). Based on our data, the use of a mix of fast-growing, generalist species with high survival rates may be best suited for increasing the success rate of restoration of the denuded areas in the Pantabangan-Carranglan Watershed. Prospective candidates include *Camellia lanceolata*, *Mangifera monandra*, *Allophyllus cobbe*, *Anisoptera thurifera*, and *Syzygium* sp. 01- all of which exhibited high abundance and growth in the MPFDP as seen in their respective spatial distribution maps (Figure 3). *Camellia lanceolata*, *A. thurifera*, and *M. monandra* are seen to be well-distributed throughout the plot. On the other hand, *A. cobbe* and *Syzygium* sp. 01 are only concentrated in specific regions of the forest plot, which may suggest more specific conditions for these species to survive. All of these species rank among the top 20 most abundant tree species in the plot. The IVI of these trees are also among the highest of all recorded tree species, indicating their ecological importance and dominance within the plot. Notably, a study on forest management highlights that IVI is a valuable tool in prioritizing species for conservation (Yilma et al., 2021). These recommended native species are thus promising candidates for restoration efforts in the country. Apart from their high growth rates and IVI, these species were also observed to have high basal areas and are thus efficient carbon sinks. Their high carbon sequestration rates may be used to combat climate change. Lastly, *M. monandra*, *A. cobbe*, and *Syzygium* sp. 01 bear fleshy fruits that can attract frugivores and greatly contribute to facilitating the natural regeneration of the watershed (Elliott et al., 2022).

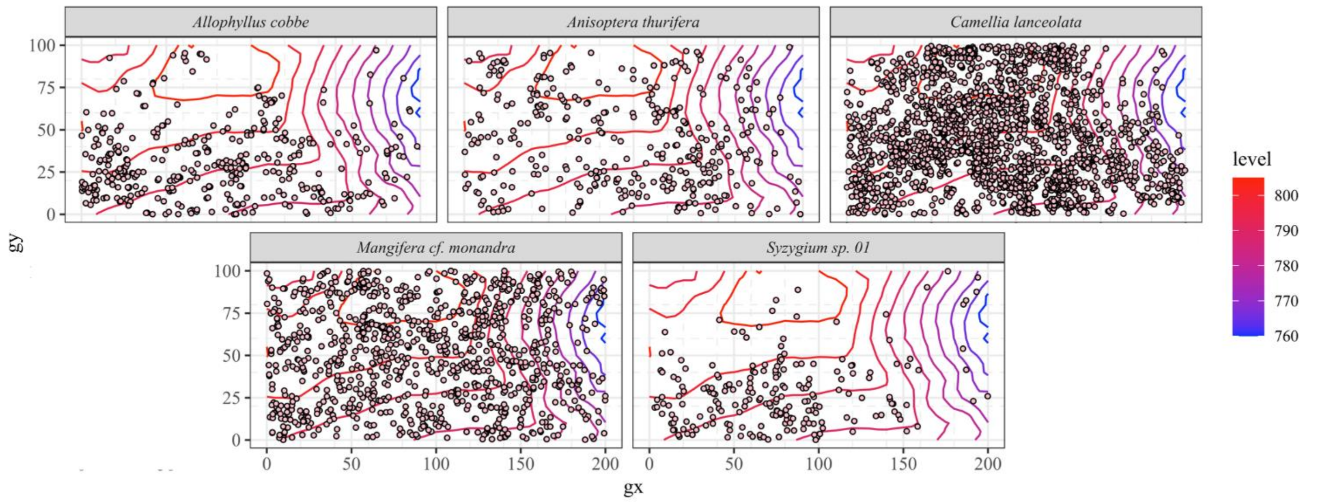

Figure 3. Spatial distribution maps of *Allophyllus cobbe*, *Anisoptera thurifera*, *Camellia lanceolata*, *Mangifera monandra*, and *Syzygium* sp. 01 in the Maluyon Permanent Forest Dynamics Plot.

5. CONCLUSION

The Maluyon Permanent Forest Dynamics Plot harbors 177 tree species belonging to 91 families and 97 genera. Tree abundance and tree density increased to 10,686 recorded individuals and 5,343 individuals per hectare in 2015. Mean growth and mortality rates were lower in the Maluyon Plot in comparison to other forest dynamics plots. The slower, overall growth rate may be associated with less disturbance and high competition brought about by high tree density. Species-specific analysis revealed the presence of two demographic trade-offs: the growth-survival and the stature-recruitment trade-offs. Demographic rates also varied as a function of size class. Small-sized trees had the lowest growth rate while large-sized trees had the highest growth rate. It was also observed that large-sized trees had lower mortality rates. Recruitment rates, on the other hand, were close to zero for all size classes. Monitoring of additional plots in other Philippine islands will give us a further understanding of the generality of these tropical forest dynamics patterns.

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