Species diversity, composition, and heterospecific associations of trees in three altitudinal gradients in Bird's Head Peninsula, Papua, Indonesia

SEPUS MARTEN FATEM¹, DONY ARISTONE DJITMAU¹, ANTONI UNGIRWALU¹, ALFREDO OTTOW WANMA¹, VICTOR IMMANUEL SIMBIAK¹, NITHANEL MIKAEL HENDRIK BENU³, JUNUS TAMBING³, AGUSTINUS MURDJOKO^{1,2,♥}

¹Faculty of Forestry, Universitas Papua. Jl. Gunung Salju Amban, Manokwari 98314, West Papua, Indonesia ²Research Center of Biodiversity, Universitas Papua. Jl. Gunung Salju Amban, Manokwari 98314, West Papua, Indonesia [•]email: agustinus.murdjoko.papua@gmail.com.

³Forestry Research and Development Agency of Manokwari. Jl. Inamberi-Susweni, Manokwari 98301, West Papua, Indonesia

Manuscript received: 29 May 2020. Revision accepted: 16 July 2020.

Abstract. Fatem SM, Djitmau DA, Ungirwalu A, Wanma AO, Simbiak VI, Benu NMH, Tambing J, Murdjoko A. 2020. Species diversity, composition, and heterospecific associations of trees in three altitudinal gradients in Bird's Head Peninsula, Papua, Indonesia. Biodiversitas 21: 3596-3605. The region of Bird's Head Peninsula, West Papua, Indonesia has a high level of vegetation diversity distributed from coastal to mountain areas. Yet, the information regarding this diversity is limited. We studied species diversity, composition, and heterospecific association of trees in three altitudinal gradients in Bird's Head Peninsula to reveal the biotic phenomenon in the region. Systematic random sampling was applied during data collection in three locations representing lower, middle, and upper altitudes of natural tropical forest. We applied diversity indices to investigate taxonomic diversity, importance value index (IVI) to reveal floristic composition and canonical correspondence analysis (CCA) for heterospecific associations. In total, we recorded 30 families, 44 genera, and 66 species in the three locations. There were 20 families in lower area and each 15 families in middle and upper areas while the genera per site were 29 in lower, 20 in the middle, and 18 in the upper. The number of species found in lower, middle, and upper areas was 35 species, 24 species, and 27 species respectively. The research revealed that the taxonomic diversity of trees generally decreases as the elevation increases in terms of family, genera, and species level. The dominant species was also different across elevation gradients in which the dominant tree had a different pattern in the three locations between understory and upperstory. Moreover, the gradient of elevation has shaped the type of tree communities, suggesting interactions and associations among tree species. Of all species recorded, 26 species were listed in IUCN Red List with two species were under data deficient, 20 species were least concern, three species were near threatened, and one species was vulnerable.

Keywords: Canonical correspondence analysis, conservation status, Pielou's evenness, Shannon-Wiener index, Vegan package

INTRODUCTION

Natural forest in tropical regions comprises a variety of ecological conditions, which can be divided into biotic and abiotic factors (Pan et al. 2013; Brown et al. 2014; Ashton 2018). The abiotic factors consist of climatic and edaphic variables, while the biotic factors consist of living organisms. The topographical arrangement of natural tropical forests varies from lower area to mountain area, resulting in variations of ecological conditions (Duivenvoorden 1995; Hunter et al. 2015; Vázquez and Givnish 1998). Consequently, the biotic factors are impacted by such variations, resulting in the gradient of biological diversity.

In tropical region, vegetation as a component of biotic factors shows differences in term of taxonomic diversity, population density, abundance, floristic composition, vertical structure and dispersal pattern (Huang et al. 2003; Phillips and Lewis 2014; Putz and Romero 2014; Addi et al. 2020). The pattern of the difference also forms vegetation communities as conspecific and heterospecific associations in which the communities create a particular characteristic (Trogisch et al. 2017; Clark et al. 2018). The

conspecific association occurs between individuals in the same species of trees such as juveniles and mature individuals (Luo et al. 2009; Murdjoko et al. 2016a). The heterospecific association is the interaction of individuals among different species of trees (Zhu et al. 2015b; Johnson et al. 2017; Atanasso et al. 2019).

Bird's Head Peninsula is located in the western part of Papua, Indonesia in which administratively the area belongs to Province of West Papua, Indonesia. The region encompasses a high variety of abiotic factors, such as topographical gradient, resulting in a high level of vegetation diversity, which is distributed from coastal areas to mountain areas. The area harbors biotic factors with high diversity of flora and fauna. However, only little has been published scientifically i.e., wildlife (Shaverdo et al. 2016; Szczepański et al. 2018; Kaiser et al. 2019; Pattiselanno et al. 2019) and vegetation (Heatubun 2002; Heatubun et al. 2009, 2013; Maturbongs et al. 2014, 2015; Sillanpää et al. 2017; Robiansyah 2018).

Most area of Bird's Head Peninsula is pristine forest as the consequence of the low accessibility. Some parts of this region have been officially assigned as conservation areas, as such the management of the forest in this region is focused on conservation purposes (Bappeda Tambrauw 2015). For example, the Tambrauw District, which is located in the Bird's Head Peninsula, has been declared as conservation district to promote the sustainability of the forest. Thus, development program of this district must consider the principle of nature conservation (Fatem and Asem 2015; Fatem et al. 2018).

Hence, to provide baseline information regarding the natural resources in Bird's Head Peninsula, particularly the vegetation conditions, research must be conducted systematically in the region as the vegetation shows different responses to different biotic and abiotic factors (Fatem and Asem 2015; Robiansyah 2018). For this rationale, we studied the taxonomic dominance of tree and heterospecific association in tropical montane forests to reveal the biotic condition. We hypothesized that taxonomic dominance differs as the consequences of the difference in elevation of tropical montane forests in Bird's Head Peninsula and the taxonomic variation of the tree communities (Ding et al. 2019). This study only focused on the tree as part of the vegetation in which the presence of the tree could explain the phenomenon of vegetation overall. We expected that this research would encourage future research in Bird's Head Peninsula to enrich scientific information to support conservation program.

MATERIALS AND METHODS

Study period and area

This research was conducted in Tambrauw Mountains, which is part of the Bird's Head Peninsula, Tambrauw District, West Papua Province, Indonesia (Figure 1). The study took place in three different sites representing three altitudes: Site A at lower area with an altitude of 488 meters above sea level (m asl) (S $0^{\circ}49'54.14''$ and E $132^{\circ}29'17.78$), B at middle altitude of 950 m asl (S $0^{\circ}43'3.49''S$ and E $132^{\circ}23'47.15''$), and C at high altitude of 1200 m asl (S $0^{\circ}40'28.82''S$ and E $132^{\circ}13'1.32''$). The area was characterized by the mountainous topography with variations in elevation and slope. The data were collected in October 2019.

Sampling and data collection

We established twenty plots of 20 m x 20 m in each research site with at least 100 m distance between plots. We then made subplots nested in each plot to measure four stages of tree growth: (i) 20 m x 20 m subplot to collect mature tree (diameter > 20 cm); (ii) 10 m x 10 m subplot to collect young tree (diameter between 10-20 cm); (iii) 5 m x 5 m subplot to collect tree sapling (diameter < 10 cm with height > 150 cm; (iv) 2 m x 2 m subplot to collect tree seedling (height < 150 cm). The first two subplots were set to sample the upperstory and while the latter two subplots were to sample understory. Data collected were the name of tree species, number of individuals, and diameter (cm). For identification of tree species, herbarium specimens were collected and sent to the Herbarium Papuaense, Forestry and Environment Research and Development Agency Manokwari and Herbarium Manokwariense Research Center of Biodiversity, Papua (MAN). University, Manokwari. The scientific names of species, genera, and families were checked based on The Plant List (TPL) (at the website: http://www.theplantlist.org/). We also checked the conservation status of the species on The International Union for Conservation of Nature's Red List of Threatened Species (at the website: https://www.iucnredlist.org/).

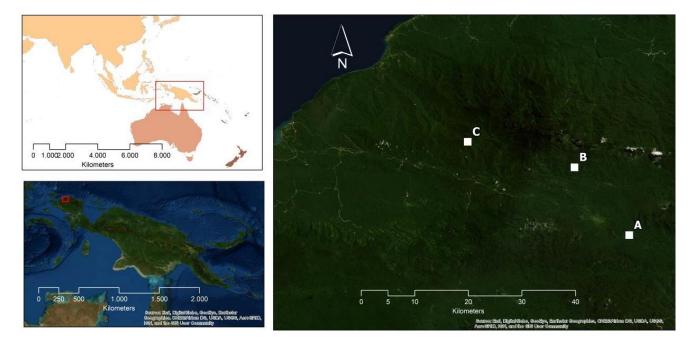


Figure 1. Location of research in three sites. The letter of A symbolizes lower area, B is middle area, and C is area with upper area based on elevation above sea level

Data analysis

The diversity in the three study sites was analyzed (Shannon 1948; Pielou 1966; Spellerberg and Fedor 2003) by calculating Shannon-Wiener diversity index as follows:

 $H' = -\sum_{i=1}^{S} p_i \ln (p_i)$

Where: H' is Shannon-Wiener diversity index, p_i is number of samples where species *i* is present.

We also calculated the evenness using Pielou's evenness as:

$$J' = H'/(\ln(S))$$

Where: S is total number of species of each location.

Taxonomic species composition was analyzed through the Importance Value Index (IVI) and calculated as follows (Curtis and McIntosh 1950; Cottam and Curtis 1956):

 $IVI_i = RFr_i + RDe_i + RDo_i$ (i.e. for the upperstory) $IVI_i = RFr_i + RDe_i$ (i.e. for the understory)

Where; IVI_i is important value index of species *i*, RFr_i is relative frequency of species *i*, RDe_i is relative density of species *i*, RDo_i is relative dominance of species *i*.

We applied Canonical Correspondence Analysis (CCA) to analyze the heterospecific associations among species in three locations (Ter Braak 1986; Murdjoko et al. 2017). This analysis was to investigate the tree communities formed in the three locations whether there was a tendency of species to present as a group or community. In the computation, we set 66 columns to fit with the total number of tree species recorded and 60 rows as the sum of plots across the tree study sites (i.e. every 20 plots in lower area, middle area, and upper area). Chi-square test (χ^2) was performed to validate the CCA. The computations used *vegan* package in R version 3.5.3 (Oksanen et al. 2019).

RESULTS AND DISCUSSION

Tree diversity

In total, we recorded 30 families, 44 genera, and 66 species in the three locations. There were 20 families in lower area and every 15 families in middle and upper areas

while the genera per site were 29 in lower, 20 in the middle, and 18 in the upper. The number of species found in lower, middle, and upper areas was 35 species, 24 species, and 27 species respectively. In the lower site, the families of *Myrtaceae*, *Anacardiaceae*, *Burseraceae*, *Lauraceae*, and *Myristicaceae* consisted of at least three species while the other families had two species or less (Figure 2). In the middle site, the families of *Myrtaceae*, and *Sapotaceae* contained at least two species. In the upper, *Myrtaceae*, *Lauraceae* and *Fagaceae* were the families that had the species number at least three. The diversity at family level was higher in the lower area compared with the two areas and the species diversity showed the same pattern as family diversity.

Species diversity varied among the three locations (Table 1). To compare tree species diversity, we grouped species at the three locations and the structure of the tree (understory and upperstory). The results revealed the decline in species diversity from the lower, middle, and upper, indicated by the decrease in Shannon-Wiener index. The pattern of species diversity of understory was similar to tree category in general, while the diversity of upperstory showed an increase from lower to middle and then slightly decline from the middle to upper. The decreasing index of Pielou's evenness occurred in all categories and understory. However, Pielou's evenness index for upperstory showed fluctuating pattern where the J' dropped from lower to middle and marginally increase from the middle to upper.

The diversity of understory is more dynamic than the diversity of upperstory since the understory comprises the juvenile phase of the tree as seedlings (Murdjoko et al. 2016b). During the seedling establishment, this period is crucial as a result of the high mortality rate of seedlings (Dong et al. 2014; Lu et al. 2014; Zhu et al. 2015c). The process can be explained that the seedlings that just germinated would compete and interact with other vegetation and also can be as food for some animals (Sinery 2013). Therefore, higher diversity tends to occur in the understory. Moreover, the decrease of diversity as elevation increase is likely due to the limited dispersal of some species to the higher elevation. Thus, the higher elevation, the less diversity of species. The dispersal of species is also affected by the seed or fruit characteristics such as height, shape, and whether edible or not for animals (Clark et al. 2018; Yguel et al. 2019).

Table 1. Shannon-Wiener Index (H') and Pielou's evenness index (J') for the three study sites (mean [standard deviation]). The letter of A symbolizes lower area, B is middle area, and C is area with upper altitude based on elevation above sea level

		Α	В	С
		(Lower area)	(Middle area)	(Upper area)
All	Η'	2.365 [0.115]	1.914 [0.101]	1.602 [0.067]
	J'	0.785 [0.007]	0.691 [0.014]	0.578 [0.006]
Upperstory	Η'	1.896 [0.044]	2.088 [0.184]	2.087 [0.054]
	J'	0.912 [0.021]	0.888 [0.053]	0.906 [0.023]
Understory	Η'	2.286 [0.160]	1.799 [0.045]	1.474 [0.001]
·	J'	0.870 [0.006]	0.781 [0.020]	0.690 [0.027]

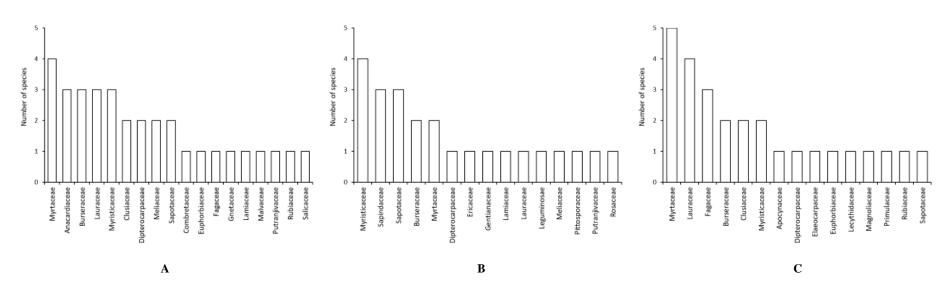


Figure 2. Number of species per family in the three study sites. The letters of A, B, and C are symbols of the lower area, middle area, and upper area, respectively.

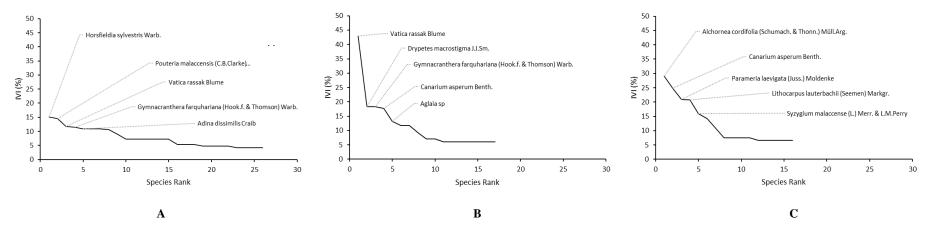


Figure 3. Top five dominant tree species for understory in the three sites based on Importance Value Index (IVI). The letter of A symbolizes lower area, B is middle area, and C is upper area.

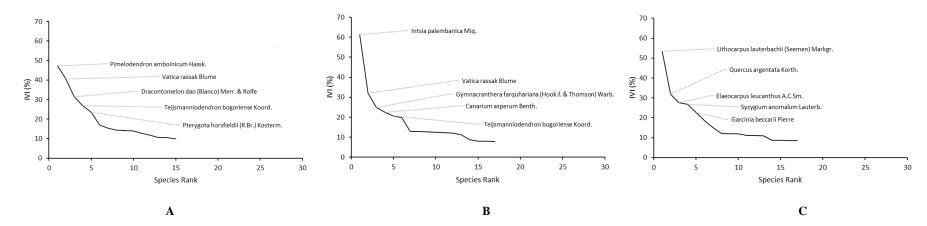


Figure 4. Top five dominant tree species for understory in the three sites based on Importance Value Index (IVI). The letter of A symbolizes lower area, B is the middle area, and C is the area upper

Dominant tree species

We compared dominant tree species across the three study sites and growth stages. The results showed that there were differences in dominant tree species not only across the three locations but also the growth stages (i.e. understory and upperstory (Figures 3 and 4). The dominant species for understory were Horsfieldia sylvestris Warb., Pouteria malaccensis (C.B.Clarke) Baehni, Vatica rassak Blume, Gymnacranthera farquhariana (Hook.f. & Thomson) Warb., and Adina dissimilis Craib in the lower study site; Vatica rassak Blume, Drypetes macrostigma J.J.Sm., Gymnacranthera farquhariana (Hook.f. & Thomson) Warb., Canarium asperum Benth., and Aglaia sp in the middle site; and Alchornea cordifolia (Schumach. & Thonn.) Müll.Arg., Canarium asperum Benth., Parameria laevigata (Juss.) Moldenke, Lithocarpus lauterbachii (Seemen) Markgr., and Syzygium malaccense (L.) Merr. & L.M.Perry in the upper site. The dominant species for upperstory were Pimelodendron amboinicum Hassk., Vatica rassak Blume, Dracontomelon dao (Blanco) Merr. & Rolfe, Teijsmanniodendron bogoriense Koord., and Pterygota horsfieldii (R.Br.) Kosterm. in the lower site; Intsia palembanica Miq., Vatica rassak Blume, Gymnacranthera farquhariana (Hook.f. & Thomson) Warb., Canarium asperum Benth., and Teijsmanniodendron bogoriense Koord. In the middle site; and Lithocarpus lauterbachii (Seemen) Markgr., Ouercus argentata Korth., Elaeocarpus leucanthus A.C.Sm., Syzygium anomalum Lauterb., and Garcinia beccarii Pierre in the upper site.

Tree communities as species interactions

We grouped tree species as communities to investigate whether there are interactions among them. We applied Canonical Correspondence Analysis (CCA) to cluster the species. We found group of species in the three study sites with the number of species in the lower area is 27 species, the middle area with 16 species, and upper area with 19 species (Figure 5). On the other hand, there are four species presented dominantly in more than one location. The density of species shaped the four tree communities in this research based on the distribution across the difference of elevation. The CCA explained the variation of 57.65 % in the first axis (CCA1) and 42.35 % in the second axis (CCA2). The validation of CCA showed that the Chisquared test (χ^2) test= 1.4611, df = 130, p-value > 0.05. Therefore, the CCA was valid to describe the heterospecific associations as the distribution phenomenon of species. The species name of abbreviations in Figure 5 can be seen in Table S1.

Regardless of the growth stage as seedlings, saplings, poles/young trees, and mature trees, some species tend to be dominant in the lower area, middle area, and upper area which explain the pattern of communities formed (Figure 5). Each species has physiological, anatomical, and phenological characteristics that affect the interactions and associations with other species (Pavón et al. 2000; Zhu et

al. 2015a; Crausbay and Martin 2016). For example, the lifespan of species affects the community formed (Zuidema et al. 2013; Jiang et al. 2015; Ganivet et al. 2020), and the seed characteristics determine the distribution of species during the dispersal which often involves animals (Naniwadekar et al. 2015; Finnegan et al. 2019). However, in this research, the ecological conditions of each location, which differs in elevation, is likely the driving factors that form tree community. The conspecific association also relate to regeneration processes which might beneficial when developing conservation program such as planting for restoration (Seidler and Plotkin 2006; Zhu et al. 2015c; Murdjoko et al. 2016a).

Distribution of individuals based on diameter class

Our study found that diameter class is not equally distributed and the distribution forms the reversed-J shape in which lower diameter trees dominated the stands than the higher diameter ones (Figure 6). This pattern is uniform across the three locations which is common in natural tropical forests. Of all young individuals with lower diameter class, only a few numbers of them that would grow to mature individuals as young individuals would compete and interact with each other to reach the canopy level as they require solar radiation (Bagchi et al. 2010; Metz et al. 2010; Zangaro et al. 2016). The competition not only occurs among individuals of trees but also other vegetation in different lifeforms such as lianas, herbs, and ferns. The competition and interaction are to obtain nutrients in soil and sunlight, so the relationship among vegetation as symbiosis (Barron et al. 2011; Taylor et al. 2019). On a broad scale, symbiosis in natural tropical forests takes place not only among vegetation but also with other organisms such as wildlife and microorganism (Silver et al. 1996; De Cáceres et al. 2013; Zhu et al. 2015c).

Therefore, the observation of size distribution between small and larger individuals is imperative to describe the regeneration process. For future research, it is crucial to analyze size distribution for certain species to figure out the natural regeneration process, so the result would be beneficial for the management of the natural tropical forest.

Conservation status

In total across the three locations, there were 26 species identified with the conservation status based on the International Union for Conservation of Nature Red List of Threatened Species (https://www.iucnredlist.org/) (Table 2). The status of data deficient (DD) was only present in the lower location (C), while at least nine species least concern (LC) status across the three locations. There were species with near threatened (NT) in the three locations, while vulnerable (VU) was only present in the lower location. Tree species with status near threatened (NT) are *Aglaia odorata* Lour., *Cryptocarya massoy* (Oken) Kosterm., and *Pouteria malaccensis* (C.B.Clarke) Baehni; and vulnerable (VU) is *Anisoptera curtisii* Dyer ex King.

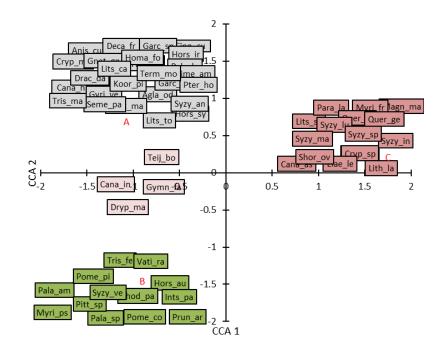


Figure 5. Canonical correspondence analysis (CCA) plot showing the heterospecific association of tree species in the three sites. The red letter of A symbolizes lower area, B is the middle area, and C is the upper area.

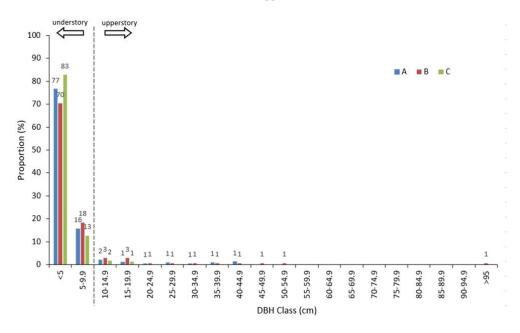


Figure 6. Distribution of individuals based on the DBH class (cm) in the three study sites displaying the understory at left side and upperstory at the right side. The letter of A symbolizes lower area, B is the middle area, and C is the upper area.

Table 2. Conservation status of tree species in the three sites based on the IUCN Red List. The letter of A symbolizes lower area, B is middle area, and C is upper area. N.A. is data not available

	Conservation status					
Locations	N.A.	Data Deficient (DD)	Least Concern (LC)	Near Threatened (NT)	Vulnerable (VU)	
А	20	0	11	3	1	
В	14	0	9	1	0	
С	14	2	9	2	0	

3603

 Table S1.
 Species name in Canonical correspondence analysis

 (CCA) plot
 (CCA)

		Plant Community A
Adin_di	:	Adina dissimilis Craib
Agla_od	:	Aglaia odorata Lour.
Agla_sp.1	:	Aglaia spectabilis (Miq.) S.S.Jain & S.Bennet
Anis_cu	:	Anisoptera curtisii Dyer ex King
Cana_hi	:	Canarium hirsutum Willd.
Cinn_cu	:	Cinnamomum culitlawan (L.) J.Presl
Cryp_ma	:	Cryptocarya massoy (Oken) Kosterm.
Deca fr		Decaspermum fruticosum J.R.Forst. & G.Forst.
Drac_da		Dracontomelon dao (Blanco) Merr. & Rolfe
Garc be		Garcinia beccarii Pierre
Garc_sp	:	Garcinia sp
Gnet_gn		Gnetum gnemon L.
Gyri_ve		Gyrinops versteegii (Gilg) Domke
Homa_fo		Homalium foetidum Benth.
Hors ir		Horsfieldia irya (Gaertn.) Warb.
Hors_sy		Horsfieldia sylvestris Warb.
Koor_pi		Koordersiodendron pinnatum Merr.
Lits_ca		<i>Litsea calophylla</i> (Miq.) Mansf.
Lits_to		Litsea tomentosa Blume
Pala_lo		Palaquium lobbianum Burck
Pime am		Pimelodendron amboinicum Hassk.
Pout_ma		Pouteria malaccensis (C.B.Clarke) Baehni
Pter_ho		Pterygota horsfieldii (R.Br.) Kosterm.
_		
Seme_pa		Semecarpus papuana Lauterb.
Syzy_an		Syzygium anomalum Lauterb. Terminalia morobensis Coode
Term_mo	-	
Tris_ma	:	Tristaniopsis macrosperma (F.Muell.) Peter
		G.Wilson & J.T.Waterh.
. 1		Plant Community B
Agla_sp		Aglaia sp
Fagr_el		Fagraea elliptica Roxb.
Harp_ar		Harpullia arborea (Blanco) Radlk.
Hors_au		Horsfieldia australiana S.T.Blake
Ints_pa		Intsia palembanica Miq.
Myri_ps		Myristica pseudoargentea Warb.
Pala_am		Palaquium amboinense Burck
Pala_sp		Palaquium sp
Pitt_sp	:	Pittosporum spinescens (F.Muell.) L.W.Cayzer,
_		Crisp & I.Telford
Pome_co		Pometia coriacea Radlk.
Pome_pi		Pometia pinnata J.R.Forst. & G.Forst.
Prun_ar		Prunus arborea (Blume) Kalkman
Rhod_pa		Rhododendron papillatum Balf. f. & R.E. Cooper
Syzy_ve		Syzygium versteegii (Lauterb.) Merr. & L.M.Perry
Tris_fe	:	Tristaniopsis ferruginea (C.T.White) Peter
		G.Wilson & J.T.Waterh.
Vati_ra	:	Vatica rassak Blume
		Plant Community C
Alch_co	:	Alchornea cordifolia (Schumach. & Thonn.)
		Müll.Arg.
Ardi_se		Ardisia serrata (Cav.) Pers.
Barr_as		Barringtonia asiatica (L.) Kurz
Cana_as		Canarium asperum Benth.
Cryp_od		Cryptocarya odorata Guillaumin
Cryp_sp	:	Cryptocarya sp
Elae_le	:	Elaeocarpus leucanthus A.C.Sm.
Lith_la	:	Lithocarpus lauterbachii (Seemen) Markgr.
Lits_sp	:	Litsea sp
Magn_ma	:	<i>Magnolia macklottii</i> (Korth.) Dandy
Myri_fr	:	Myristica fragrans Houtt.
	-	

Para_la	: Parameria laevigata (Juss.) Moldenke
Quer_ar	: Quercus argentata Korth.
Quer_ge	: Quercus gemelliflora Blume
Shor_ov	: Shorea ovalis Blume
Syzy_in	: Syzygium inophyllum DC.
Syzy_lu	: Syzygium luehmannii (F.Muell.) L.A.S.Johnson
Syzy_ma	: Syzygium malaccense (L.) Merr. & L.M.Perry
Syzy_sp	: Syzygium sp
	Plant Community OTHER
Cana_in	: Canarium indicum L.
Dryp_ma	: Drypetes macrostigma J.J.Sm.
Gymn_fa	: Gymnacranthera farquhariana (Hook.f. &
-	Thomson) Warb.
Teij_bo	: Teijsmanniodendron bogoriense Koord.

The four species with conservation status of near threatened and vulnerable were less dominant species except for *P. malaccensis*. Hence, those should be in consideration in the management of the natural tropical forest. For example, future research should focus on the dispersal, regeneration, and the utilization of those species (Vlam et al. 2017; Padmakumar et al. 2018; Li et al. 2020). This could be one of the conservation programs to support the conservation district of Tambrauw. Besides, the species with conservation status not available need to be studied to gain more scientific information. Furthermore, the concept of forest conservation could be implemented widely not only focusing on biotic such as vegetation but the socio-culture aspect could be also considered (Ungirwalu et al. 2014, 2017).

ACKNOWLEDGMENTS

The authors are extremely grateful to Tambrauw District for financial support during the research. We also thank anonymous reviewers for improving this article.

REFERENCES

- Addi A, Soromessa T, Bareke T .2020. Plant diversity and community analysis of Gesha and Sayilem forest in Kaffa Zone, Southwestern Ethiopia. Biodiversitas 21:2878–2888.
- Ashton P .2018. What future for Asia's lowland tropical evergreen forests? J Trop For Sci 30:418–423.
- Atanasso JA, Mensah S, Azihou AF, et al. 2019. Heterospecific Tree Density and Environmental Factors Affect Afzelia africana Sm. Population Structure in the Pendjari Biosphere Reserve, West Africa: Implications for Management and Restoration. Trop Conserv Sci 12:.
- Bagchi R, Press MC, Scholes JD .2010. Evolutionary history and distance dependence control survival of dipterocarp seedlings. Ecol Lett 13:51–59.
- Bappeda Tambrauw, 2015. Rencana Tata Ruang Wilayah Revisi Kabupaten Tambrauw [Indonesian].
- Barron AR, Purves DW, Hedin LO .2011. Facultative nitrogen fixation by canopy legumes in a lowland tropical forest. Oecologia 165:511–520.
- Brown S, Lugo AE, Brown S, et al .2014. Tropical secondary forests. 6:1-32
- Clark AT, Detto M, Muller-Landau HC, et al .2018. Functional traits of tropical trees and lianas explain spatial structure across multiple scales. J Ecol 106:795–806.

- Cottam G, Curtis J. T. .1956. The Use of Distance Measures in Phytosociological Sampling. Ecology 37:451–460
- Crausbay SD, Martin PH .2016. Natural disturbance, vegetation patterns and ecological dynamics in tropical montane forests. J Trop Ecol 32:384–403.
- Curtis J, McIntosh R .1950. The Interrelations of Certain Analytic and Synthetic Phytosociological Characters. Ecology 31:434–455
- De Cáceres M, Legendre P, He F .2013. Dissimilarity measurements and the size structure of ecological communities. Methods Ecol Evol 4:1167–1177.
- Ding Y, Zang R, Lu X, Huang J .2019. Functional features of tropical montane rain forests along a logging intensity gradient. Ecol Indic 97:311–318.
- Dong TL, Beadle CL, Doyle R, Worledge D .2014. Site conditions for regeneration of hopea odorata in natural evergreen dipterocarp forest in Southern Vietnam. J Trop For Sci 26:532–542
- Duivenvoorden JE .1995. Tree species composition and rain forestenvironment relationships in the middle Caquetá area, Colombia, NW Amazonia. Vegetatio 120:91–113.
- Fatem SM, Asem G .2015. Kabupaten konservasi sebagai political action pemerintah daerah dalam mendukung konservasi sumberdaya alam hayati: Studi kasus Kabupaten Tambrauw, Papua Barat. Pros Sem Nas Masy Biodiv Indon 1:1403–1410.
- Fatem SM, Awang SA, Pudyatmoko S, et al .2018. Camouflaging economic development agendas with forest conservation narratives: A strategy of lower governments for gaining authority in the recentralising Indonesia. Land Use Pol 78:699–710.
- Finnegan L, Pigeon KE, MacNearney D .2019. Predicting patterns of vegetation recovery on seismic lines: Informing restoration based on understory species composition and growth. For Ecol Manage 446:175–192.
- Ganivet E, Unggang J, Bodos V, et al .2020. Assessing tree species diversity and structure of mixed dipterocarp forest remnants in a fragmented landscape of north-western Borneo, Sarawak, Malaysia. Ecol Indic 112:106117.
- Heatubun CD .2002. A Monograph of Sommieria. Arecaceae. Kew Bull 57:599–611
- Heatubun CD, Baker WJ, Mogea JP, et al .2009. A monograph of Cyrtostachys. Arecaceae. Kew Bull 64:67–94.
- Heatubun CD, Iwanggin MP, Simbiak VI .2013. A new species of betel nut palm. Areca: Arecaceae. from western New Guinea. Phytotaxa 154:59–64.
- Huang W, Pohjonen V, Johansson S, et al .2003. Species diversity, forest structure and species composition in Tanzanian tropical forests. For Ecol Manage 173:11–24.
- Hunter MO, Keller M, Morton D, et al .2015. Structural dynamics of tropical moist forest gaps. PLoS One 10:1–19.
- Jiang Y, Zang R, Lu X, et al .2015. Effects of soil and microclimatic conditions on the community-level plant functional traits across different tropical forest types. Plant Soil 390:351–367.
- Johnson DJ, Condit R, Hubbell SP, Comita LS .2017. Abiotic niche partitioning and negative density dependence drive tree seedling survival in a tropical forest. Proc R Soc B Biol Sci 284.
- Kaiser CM, O'Shea M, Kaiser H .2019. A new species of Indo-Papuan groundsnake, genus Stegonotus Duméril et al., 1854 .Serpentes, Colubridae., from the Bird's Head Peninsula of West Papua, Indonesia, with comments on differentiating morphological characters. Zootaxa 4590:201–230. https://doi.org/10.11646/zootaxa.4590.2.1
- Li C, Chen Y, Yang F, et al .2020. Population structure and regeneration dynamics of Firmiana major, a dominant but endangered tree species. For Ecol Manage 462:117993.
- Lu X, Zang R, Ding Y, et al .2014. Variations and trade-offs in functional traits of tree seedlings during secondary succession in a tropical lowland rain forest. Biotropica 46:404–414.
- Luo Z, Ding B, Mi X, et al .2009. Distribution patterns of tree species in an evergreen broadleaved forest in eastern China. Front Biol China 4:531–538.
- Maturbongs RA, Dransfield J, Baker WJ .2014. Calamus kebariensis .Arecaceae.-a new montane rattan from New Guinea. Phytotaxa 163:235–238. https://doi.org/10.11646/phytotaxa.163.4.4
- Maturbongs RA, Dransfield J, Mogea JP .2015. Daemonorops komsaryi .Arecaceae.—A new rattan from the Bird's Head Peninsula, Indonesian New Guinea. Phytotaxa 195:297–300.

- Metz MR, Sousa WP, Valencia R .2010. Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. Ecology 91:3675–3685.
- Murdjoko A, Marsono D, Sadono R, Hadisusanto S .2016a. Plant Species Composition and Their Conspecific Association in Natural Tropical Rainforest, South Papua. Biosaintifika J Biol Biol Educ 8:33.
- Murdjoko A, Marsono D, Sadono R, Hadisusanto S .2017. Recovery of residual forest ecosystem as an impact of selective logging in South Papua: An ecological approach. Biotropia 24:230–245.
- Murdjoko A, Marsono D, Sadono R, Hadisusanto S .2016b. Tree Association with Pometia and its Structure in Logging Concession of South Papua Forest. J Manaj Hutan Trop 22:180–191.
- Naniwadekar R, Shukla U, Isvaran K, Datta A .2015. Reduced hornbill abundance associated with low seed arrival and altered recruitment in a hunted and logged tropical forest. PLoS One 10:e0120062.
- Oksanen J, F. Guillaume Blanchet RK, Legendre P, et al .2019. Package 'vegan.' R Packag version 340
- Padmakumar B, Sreekanth NP, Shanthiprabha V, et al .2018. Tree biomass and carbon density estimation in the tropical dry forest of southern Western Ghats, India. iForest 11:534–541.
- Pan Y, Birdsey RA, Phillips OL, Jackson RB .2013. The Structure, Distribution, and Biomass of the World's Forests. Annu Rev Ecol Evol Syst 44:593–622.
- Pattiselanno F, Apituley JRM, Arobaya AYS, Koibur JF .2019. Short communication: Using wildlife for local livelihood - Experiences from the bird's head Peninsula, West Papua, Indonesia. Biodiversitas 20:1839–1845. DOI: 10.13057/biodiv/d200708
- Pavón NP, Hernández-Trejo H, Rico-Gray V .2000. Distribution of plant life forms along an altitudinal gradient in the semi-arid valley of Zapotitlán, Mexico. J Veg Sci 11:39–42.
- Phillips OL, Lewis SL .2014. Recent changes in tropical forest biomass and dynamics. For Glob Chang 77–108.
- Pielou EC .1966. The measurement of diversity in different types of biological collections. J Theor Biol 13:131–144.
- Putz FE, Romero C .2014. Futures of tropical forests .sensu lato.. Biotropica 46:495–505.
- Robiansyah I .2018. Diversity and biomass of tree species in Tambrauw, West Papua, Indonesia. Biodiversitas 19:377–386.
- Seidler TG, Plotkin JB .2006. Seed dispersal and spatial pattern in tropical trees. PLoS Biol 4:2132–2137.
- Shannon CE .1948. A Mathematical Theory of Communication. Bell Syst Tech J 27:623–656.
- Shaverdo H, Panjaitan R, Balke M .2016. Exocelina ransikiensis sp. nov. from the Bird's Head of New Guinea. Coleoptera: Dytiscidae: Copelatinae.. Acta Entomol Musei Natl Pragae 56:103–108
- Sillanpää M, Vantellingen J, Friess DA .2017. Vegetation regeneration in a sustainably harvested mangrove forest in West Papua, Indonesia. For Ecol Manage 390:137–146.
- Silver WL, Brown S, Lugo AE .1996. Effects of changes in biodiversity on ecosystem function in tropical forests. Conserv Biol 10:17–24.
- Sinery AS .2013. Cuscus population dynamics in tourist island of Ahe, District of Nabire, Papua. Biodiversitas 14:95–100.
- Spellerberg IF, Fedor PJ .2003. A tribute to Claude-Shannon .1916-2001. and a plea for more rigorous use of species richness, species diversity and the "Shannon-Wiener" Index. Glob Ecol Biogeogr 12:177–179.
- Szczepański WT, Vondráček D, Seidel M, et al .2018. High diversity of Cetiocyon beetles. Coleoptera : Hydro- philidae. along an elevational gradient on Mt . Wilhelm, New Guinea, with new records from the Bird 's Head Peninsula. Arthropod Syst Phylogeny 76:323–347
- Taylor BN, Chazdon RL, Menge DNL. 2019. Successional dynamics of nitrogen fixation and forest growth in regenerating Costa Rican rainforests. Ecology 100:1–13.
- Ter Braak CJF .1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.
- Trogisch S, Schuldt A, Bauhus J, et al .2017. Toward a methodical framework for comprehensively assessing forest multifunctionality. Ecol Evol 7:10652–10674.
- Ungirwalu A, Awang SA, Murdjoko A .2014. Model Aplikasi Agroforestri Tumbuhan Buah Hitam .Haplolobus monticola Husson. Berbasis Pengetahuan Lokal Etnis Wandamen-Papua: Prospek Pengembangan Perhutanan Sosial di Papua. Pros Semin Nas Silvikultur II Pembaharuan Silvikultur untuk mendukung Pemulihan Fungsi Hutan menuju Ekon Hijau 268–273
- Ungirwalu A, Awang SA, Suryanto P, Maryudi A .2017. The ethnotechno-conservation approach in the utilization of Black Fruit.

Haplolobus sp., by the Wandamen ethnic of Papua, Indonesia. Biodiversitas 18:1336–1343.

- Vázquez G JA, Givnish TJ .1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. J Ecol 86:999–1020.
- Vlam M, van der Sleen P, Groenendijk P, Zuidema PA .2017. Tree age distributions reveal large-scale disturbance-recovery cycles in three tropical forests. Front Plant Sci 7:1–12. https://doi.org/10.3389/fpls.2016.01984
- Yguel B, Piponiot C, Mirabel A, et al .2019. Beyond species richness and biomass: Impact of selective logging and silvicultural treatments on the functional composition of a neotropical forest. For Ecol Manage 433:528–534.
- Zangaro W, Lescano LEAM, Matsuura EM, et al .2016. Differences between root traits of early- and late-successional trees influence

below-ground competition and seedling establishment. J Trop Ecol 32:300-313.

- Zhu H, Yong C, Zhou S, et al .2015a. Vegetation, floristic composition and species diversity in a tropical mountain nature reserve in southern Yunnan, SW China, with implications for conservation. Trop Conserv Sci 8:528–546.
- Zhu Y, Comita LS, Hubbell SP, Ma K .2015b. Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. J Ecol 103:957–966.
- Zhu Y, Comita LS, Hubbell SP, Ma K .2015c. Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. J Ecol 103:957–966.
- Zuidema PA, Baker PJ, Groenendijk P, et al .2013. Tropical forests and global change: Filling knowledge gaps. Trends Plant Sci 18:413–419.