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Heterospecific and conspecific associations of trees in lowland tropical forest of New Guinea

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Abstract. *Murdjoko A, Jitmau MM, Djitmau DA, Siburian RHS, Ungirwalu A, Wanma AO, Mardiyadi Z, Rumatora A, Mofu WY, Sineri AS, Fatem SM, Worabai D, May NL, Tokede MJ, Warmetan H, Wanggai CB, Wanma JF, Sirami EV, Paembonan JB, Unenor E, Kuswandi R, Lekitoo K, Khayati L, Benu NMH, Tambing J, Saragih ASB. 2020. Heterospecific and conspecific associations of trees in lowland tropical forest of New Guinea. Biodiversitas 21: 4405-4418.* The vegetation in the tropical rainforest of New Guinea consists of a large number of species that interact with each other within and among species. While several studies have attempted to reveal the diversity of flora of New Guinea, little is known about plant communities that develop associations. This study aimed to investigate the associations of tree species in lowland tropical forest in New Guinea. The associations depicted in this study were in the form of conspecific associations (among small and large individuals within same species) and heterospecific (among individuals of different species and divided into under and upper story). We established 48 rectangular plots created in Murkim and Teiraplu as part of Pegunungan Bintang District, Papua Province. Canonical correspondence analysis (CCA) was used to analyze heterospecific and conspecific associations. The results showed that the understory and upper story vegetation had different patterns of heterospecific association. The understory configured three heterospecific associations, consisting of 5, 13, and 90 species, while the upper story formed four heterospecific associations with 4, 8, 11, and 63 species. The analysis of conspecific associations showed of 149 tree species recorded in the study sites, only 66 species that had both small and large individuals, displaying the pattern of conspecific association. Among them, 41 species had positive associations while 25 species had negative associations. Our findings enrich the knowledge in theoretical ecology of tropical forests, especially in New Guinea.

Keywords: Canonical correspondence analysis, CCA, Papuasia, tree community, tropical rainforest, vegan package

INTRODUCTION

Tropical rainforest is a complex ecosystem with many interactions between abiotic and biotic factors, particularly among vegetation (Vitousek 1984; Thomas and Baltzer 2002; Hunter et al. 2015). This complexity results in the vegetation that consists of many life forms from vertical and horizontal compositions that interact with each other to obtain sunlight, soil nutrients, and water, and to adapt with microclimatic conditions (Slik et al. 2015, 2018; Murdjoko et al. 2016a). The interactions among vegetation have occurred over a long period due to successional process (Fernández-Lugo et al. 2015). Where the vegetation shares the same ecological condition, the morphological and physiological characters become the driving factors of behavior in the natural tropical rainforest (Gustafsson et al. 2016; Johnson et al. 2017).

The interactions among vegetation elements in the tropical rainforest in some cases represent symbiosis and inter and intra-species relationships (Legendre and Fortin 1989; Magrach et al. 2014). These interactions can be in the form of competition and association. In old tropical rainforest, the interaction occurs intensively due to the absorption of light and water, where both are the primary growth factors (Yamamoto 2000; Montgomery and Chazdon 2001). In secondary forest, canopy gap is very open, leading to more light penetrating the forest floor (Itoh et al. 1997; Angelini et al. 2015; Murdjoko et al. 2017).

The association in vegetation communities can be in the form of conspecific or heterospecific and the form of association determines the pattern of the spatial distribution of forest ecosystems either. Conspecific association is the interaction of individuals of similar species while heterospecific occurs among different species of vegetation

(Zhu et al. 2015; Wang et al. 2018). Conspecific and heterospecific associations occur during the successional process of the tropical rainforest (Farneda et al. 2018). Some studies explained that the association, either the conspecific or the heterospecific could be in a positive or negative pattern (Castilla et al. 2016).

Vegetation is distributed geographically with the diversity and pattern of plant communities that adapt to particular ecological niche (Brummitt 2001; Pan et al. 2013). Phytogeographic regions, including mainland New Guinea, have been studied for centuries. The vegetation in New Guinea spreads from coastal to high land areas, containing various types of ecosystems (Cámara-Leret and Dennehy 2019). As the result, New Guinea contains the highest diversity of flora, such as trees, climbers, shrubs, ferns, rattan, etc. (Murdjoko et al. 2016a) in which about 60% of the species are endemic (Cámara-Leret et al. 2020). For example, a forest area in New Guinea consists of a high diversity of tree species with more than 70 species per hectare that could be found (Robiansyah 2018; Fatem et al. 2020). While recently more and more studies have attempted to reveal the diversity of flora of New Guinea, little is known about plant communities that develop associations among them.

This study aimed to investigate the association of tree species in the lowland tropical forest in New Guinea. The associations depicted in this study were in the form of conspecific associations (among small and large individuals within same species) and heterospecific (among individuals of different species and divided into under and upper story). We hypothesized that the small and large tree species have heterospecific associations within the natural tropical rain forest. This kind of study is important to provide specific contribution of ecological research in the tropical rainforest of Southeast Asia, more specifically the New Guinea region (Brummitt 2001).

MATERIALS AND METHODS

Study period and area

This study was conducted in the northern part of Pegunungan Bintang District (Ind.: *kabupaten*), Papua Province, Indonesia (Figure 1). The study sites were located at Murkim (4°0'0.53"S and 140°49'17.24"E) and Teiraplu (3°59'13.46"S and 140°26'0.06"E) at an altitude of 155 m and 233 m above sea level (m asl), respectively. The ecosystem type of the two study sites are categorized as lowland areas where the southern part is bordered with the mountain range and the northern part is bordered with hills while the western and eastern parts are lowlands. Broadleaves and mixed forests are the dominant vegetation in this area, while the soil is grouped as Ultisols and Inceptisol. The climatic conditions are considered to be very humid with average temperature of 25° C for annual, 20.6° C for daily, and 16.3° C for minimum, and with monthly and annual average rainfall of 448.75 mm and 5385 mm, respectively (Kartikasari et al. 2012).

Sampling and data collection

Data were collected using sampling plot method with size of each plot 20 m x 20 m. In total, there were 48 rectangular plots established in which 24 plots were in Teiraplu and 24 plots were in Murkim. In both locations, the plots were placed to north directions at a distance of 100 m away from each other. In the 20 m x 20 m plot (A) we recorded and measured old trees with a diameter of more than 20 cm, and within this plot we established three nested sub-plots with size 10 m x 10 m (B) to record tree with diameter between 10 cm and 20 cm, size 5 m x 5 m (C) to record trees taller than 1.5 m, and size 2 m x 2 m (D) to record the species shorter than 1.5 m. The vegetation in plots A and B were classified as upper story and that in plots C and D were categorized as understory. For the understory vegetation, we recorded data of taxonomic names of every species and number of individuals, and while for the upper story vegetation we recorded data of taxonomic names of every species, number of individuals, and diameter (cm).

For identification, we collected the specimens of the plant and sent it to the Herbarium Papuaense of *Balai Penelitian dan Pengembangan Lingkungan Hidup dan Kehutanan (BP2LHK)* Manokwari and Herbarium Manokwariense (MAN) *Pusat Penelitian Keanekaragaman Hayati Universitas Papua (PPKH-UNIPA)*, Manokwari. The species name was updated according to The Plant List (TPL) at the website of http://www.theplantlist.org/.

Statistical analysis

The heterospecific and conspecific associations were analyzed using the canonical correspondence analysis (CCA) (Ter Braak 1986; Caceres and Legendre 2009), and the chi-square test (χ^2) was implemented to validate the model of CCA (Fatem et al. 2020). Furthermore, this association used the number of each individual (density) as a value in which the columns were the species and the rows were the 48 plots. The conspecific association correlated the under and upper story as small and large individuals. The columns represented the species, while the 48 plots under and upper story represented the rows. The species that did not have under and upper stories were otherwise excluded. The result of CCA displayed species in the graph with the position in the two axes. To investigate the conspecific association whether it was positive or negative, the Euclidean distance between each species as well as the under and upper stories were conducted (Murdjoko et al. 2016b, 2017). If the result of Euclidean distance of species is below the average, then the conspecific association is said to be positive, and vice versa. The vegan package in R version 3.5.3 was used to calculate the statistical analysis (Oksanen et al. 2019).

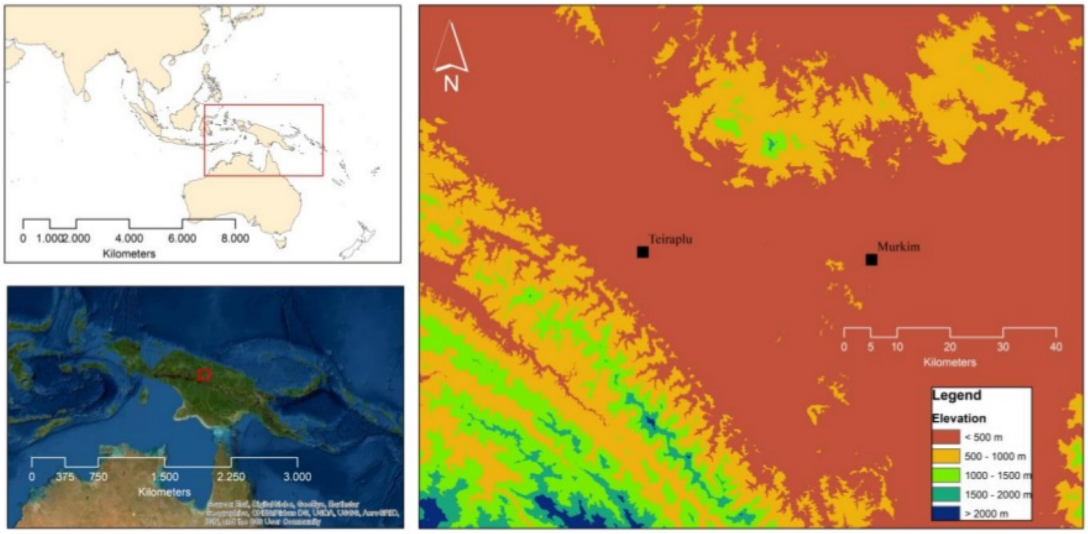

Figure 1. Map of the study sites in Teiraplu and Murkim, Pegunungan Bintang, Papua, Indonesia

RESULTS AND DISCUSSION

Heterospecific associations

The heterospecific association was grouped into two: understory and upper story, based on the structure of trees in tropical forests. As such, the analyses of multivariate statistics for the understory and upper story were separated since the natural tropical rainforest is complex with the vegetation structures forming the ecosystem. The structure was also simplified by distinguishing them into two main parts.

From the CCA result, the understory and upper story showed different patterns of heterospecific association. The understory configured three groups of communities based on species as the structure of the associations. The three groups are shown in Figure 2.

The results showed that 108 species of trees formed the association in natural tropical forests, and was valid statistically as χ^2 = 10.686, df = 2461, p-value = 1. The species of understory showed heterospecific associations as tree groups where the first consisted of 90 species (blue boxes), the second contained 13 (green boxes), and the third comprised of 5 species (red boxes) (Figure 2). The name of the species in the boxes in Figure 2 was abbreviated and the complete name can be seen in Table S1.

The CCA result showed that the upper story vegetation community had a pattern of association with a valid result of χ^2 = 11.344, df = 1955, p-value = 1. The upper story consisted of 86 species which formed four heterospecific associations, consisting of the first group (63 species) in the grey boxes, second group (11 species) in the red boxes, third group (8 species) in the purple boxes, and fourth group (4 species) in the blues boxes (Figure 3). The complete name of species presented in Figure 3 can be seen in Table S2.

The association pattern of the understory and upper story differed from one another even though they grew in the same natural forest. The difference in association has likely resulted from the variation of the vertical structure of the tropical forest. The upper story vegetation has reached the emergent layers of forest canopy, allowing species to benefit by getting more sunlight (Murdjoko et al. 2016a, 2017; Fatem et al. 2020). The formation of understory was caused by competition due to it below the canopy layers with low solar radiation (Rüger et al. 2011; Laurans et al. 2014; Angelini et al. 2015).

For centuries, the formation of tropical forests has been a sequential process in which large numbers of species compete dynamically each other (Brown et al. 1990; Wright and Muller-Landau 2006; Liu and Slik 2014; Almeida et al. 2019). The heterospecific association can be related to the fact that trees interact with each other to form symbiosis with other life forms, such as liana, fern, herb, epiphyte, etc. (Johnson et al. 2017; Cirimwami et al. 2019; Steege et al. 2019). The primary factor influencing the pattern of tree communities of understory and upper story during tropical forest succession was probably caused by the abiotic factors, especially to gain nutrients, water, and sunlight as materials to support metabolisms, especially photosynthesis. Nonetheless, many studies showed that the morphological and physiological characters have also affected different responses of species to grow and develop (Goodale et al. 2012; Gustafsson et al. 2016). For example, the nature of shade tolerance species may be a factor that allows small tree species to survive the competition and obtain limited sunlight below the canopy layers (Givnish 1999; Montesinos-Navarro et al. 2018). Therefore, it is crucial to study the shade-tolerant characters of a species in the rainforest in order to explain forest dynamics in more detail. This study is unable to reveal such characters concerning the light competition because that is beyond the scope is this study.

Conspecific associations

The analysis of conspecific associations was conducted using 149 species that grew in the study sites, but only 66 species that had small and large individuals as understory and upper story. The result of CCA showed statistically valid result as χ^2= 5.8784, df = 2904, p-value = 1 (Figure 4). In addition, it displayed the pattern of conspecific association as 41 species had positive association while 25 species had negative association. In the positive association, the small and large individuals of the 41 species were distributed closely in the same area, representing the tendency of mature trees to reproduce and germinate. Conversely, in the negative association, the small individuals of the 25 species grew mainly far from the large ones that represent the matured trees. The full list of the taxonomic name of the species in Figure 4 is presented in Table S3, and the conspecific association can be used to analyze their density dependence since the tropical forest is the place for the high diversity of trees.

Of 149 species, 83 species did not have either small or large individuals, suggesting that the species experienced poor regeneration. Some large individuals act as putative parent trees, even though they have failed to establish seedlings due to many factors (Seidler and Plotkin 2006; Rahman and Tsukamoto 2015). One possible factor is caused by the competition of seedlings with other plants on the forest floor, on which many life forms are found. Another rationale is that the seeds and seedlings are eaten by herbivores (Swaine et al. 1987; Houter and Pons 2014). Many studies have reported that herbivores are found in tropical rainforest since the forest provides a lot of food, for example, during germination, the dicotyledonous tree plants develop shoot from the plumule of the germinating seed (Houter and Pons 2014; Sawada et al. 2015).

The distribution of individual trees in tropical forests is influenced by the ability to interact with other species. This pattern of conspecific association should be studied frequently to figure out the method of regeneration and distribution of species. Forest floor encompasses many species with different life forms as a strategy to survive and grow during the competition (Dezzotti et al. 2019). Many lianas and climbers grow fast to occupy the forest canopy and space available for sunlight. These plants suppress a certain seedling establishment (Carreño-Rocabado et al. 2012). The competition to gain sunlight, nutrition, and water is presumed as the limiting factor suffered by some species since they cannot survive below putative parent trees.

Seed dispersal can be the driving force behind the spatial distribution of plants in tropical forests. Moreover, the morphological and anatomical characters of seeds and fruits also influence species regeneration and distribution. For example, small and winged seeds of tree species can spread out by falling around and away from the parent trees (Sebbenn et al. 2008; Lü and Tang 2010). However, factors such as competition, herbivory, and allelopathy have led to a clear and negative association in natural tropical forests (Padmanaba and Corlett 2014; Menezes et al. 2019). In contrast, large seeds mostly fall around the parent trees and since they survived germination, they can grow as positive conspecific associations. Therefore, the conspecific association pattern should be studied to know the natural regeneration of certain species in tropical rainforest.

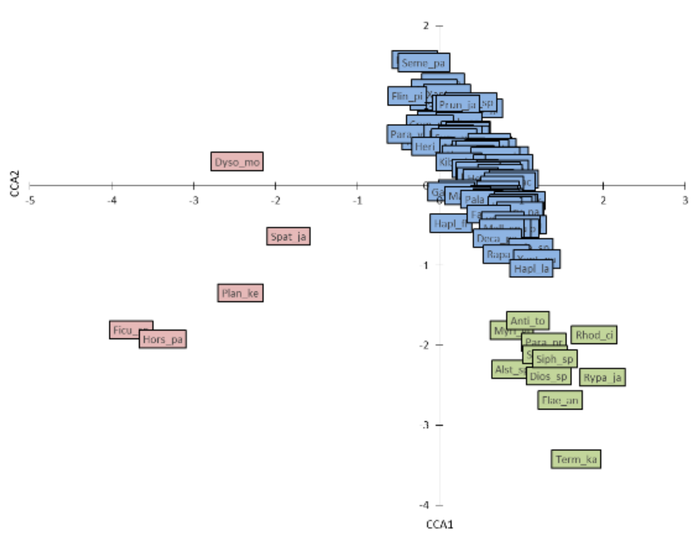

Figure 2. The result of Canonical Correspondence Analysis (CCA) to analyze the heterospecific associations for understory.

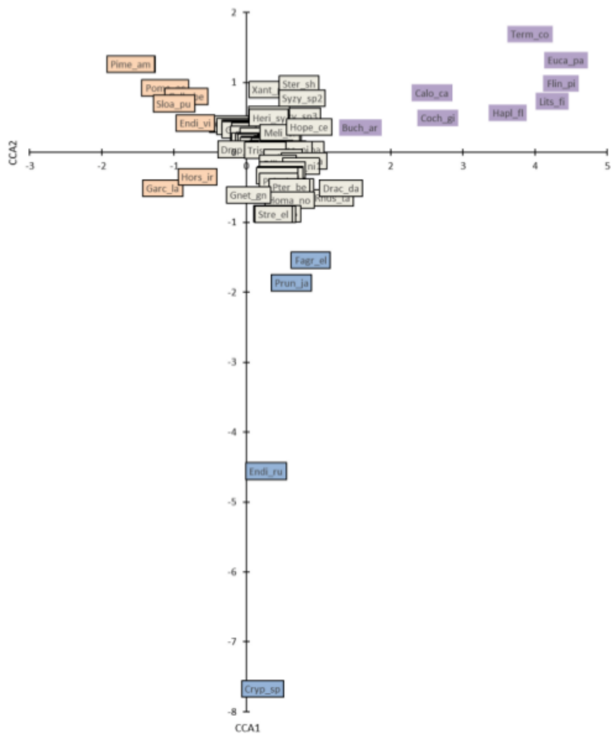

Figure 3. The result of Canonical Correspondence Analysis (CCA) to analyze the heterospecific associations for the upper story

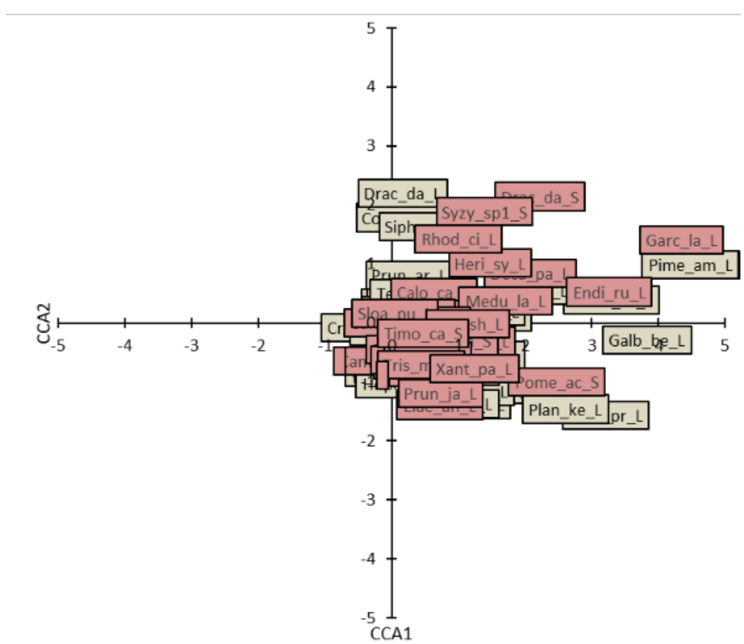

Figure 4. The result of Canonical Correspondence Analysis (CCA) to analyze conspecific associations between the small and the large individuals of the same species

The implication of associations to ecological knowledge for sustainable management of primary forest

The study of conspecific and heterospecific associations in tropical rainforest is extremely important to determine the spatial distribution pattern, especially the conspecific association. In addition, a model of natural regeneration of tree species can be described, and the result can indicate the pattern of recruitment in the population dynamics of tree species (Goodale et al. 2012; Piotto et al. 2019). Tropical rainforest is primarily dominated by flowering plants with their reproduction season is in annual period (Baker et al. 1998; Pan et al. 2013; Cámara-Leret et al. 2020). Furthermore, a suitable area for certain species to grow has resembled in the conspecific association since the study correlates small individuals with the large ones within the same species. The pattern of conspecific association can also be used to observe natural regeneration. For example, the most appropriate area to plant tree species *in-situ* conservation programs can be decided when artificial regeneration is necessary (Armstrong et al. 2011; Vergara-Rodrígue et al. 2017). The heterospecific association describes the pattern of growth in tropical rainforest since the forest includes the great diversity of tree species. The forest took several decades to develop, and this present study has been able to analyze the pattern of tree species association. Ecological studies on the theme of species association in tropical rainforest need to be replicated in other contexts of region, ecosystem type and forest conditions as tropical forest is very complex as made up of different life forms that interact and create vertical and horizontal structures in the climax phase of the successional process (Chazdon 2003; Brokaw and Scheiner 2012).

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REFERENCES

Almeid DRA, Stark SC, Schietti J, Camargo JLC, Amazonas NT, Gorgens EB, Rosa DM, Smith MN, Valbuena R, Saleska S, Andrade A, Mesquita R, Laurance SG, Laurance WF, Lovejoy TE, Broadbent EN, Shimabukuro YE, Parker GG, Lefsky M, Silva CA, Brancalion PHS. 2019. Persistent effects of fragmentation on tropical rainforest canopy structure after 20 Yr of Isolation. Ecol Appl 29 (6): 1221-1235.

Angelini, Alice, Corona P, Chianucci F, Portoghesi L. 2015. Structural attributes of stand overstory and light under the canopy. Ann Silvicultural Res 39 (1): 23-31.

Armstrong AH. Shugart HH, Fatoyinbo TE. 2011. Characterization of community composition and forest structure in a Madagascar lowland rainforest. Trop Conserv Sci 4 (4): 428-444.

Baker WJ, Coode MJE, Dransfield J, Dransfield S, Harley MM, Hoffmann P, Johns RJ. 1998. Patterns of distribution of Malesian vascular plants. Biogeogr Geol Evol SE Asia 243-258.

Brokaw NVL, Scheiner SM. 2012. Species composition in gaps and structure of a tropical forest. Ecology 70 (3): 538-541.

Brown S, Lugo AE, Brown S, Hall M, Gregory W, Lugo AE. 1990. Tropical secondary forests. J Trop Ecol 6 (1): 1-32.

Brummitt RK. 2001. World Geographical Scheme for Recording Plant Distributions. International Working Group on Taxonomic Databases For Plant Sciences (TDWG). Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh

Caceres MD, Legendre P. 2009. Associations between species and groups of sites: Indices and statistical inference. Ecology 90 (12): 3566-3574.

Cámara-Leret, Rodrigo, Dennehy z. 2019. Indigenous knowledge of New Guinea's useful plants: A review. Econ Bot 73 (3): 405-415.

Cámara-Leret, Rodrigo, Frodin DG, Adema F, Anderson C, Appelhans MS, Argent G, Guerrero SA, Ashton P, Baker WJ, Barfod AS, Barrington D, Borosova R, Bramley GLC, Briggs M, Buerki S, Cahen B, Callmander MW, Cheek M, Cheng-Wei C, Conn BJ, Coode MJE, Darbyshire I, Dawson S, Dransfield J, Drinkell C, Duyfjes B, Ebihara A, Ezedin Z, Long-Fei F, Gideon O, Girmansyah D, Govaerts R, Fortune-Hopkins H, Hassemer G, Hay A, Heatubun CD, Hind DJN, Hoch P, Homot P, Hovenkamp P, Hughes M, Jebb M, Jennings L, Jimbo T, Kessler M, Kiew R, Knapp S, Lamei P, Lehnert M, Lewis GP, Linder HP, Lindsay S, Low TW, Lucas E, Mancera JP, Monro AK, Moore A, Middleton DJ, Nagamasu H, Newman MF, Lughadha EN, Melo PHA, Ohlsen DJ, Pannell CM, Parris B, Pearce L, Penneys DS, Perrie LR, Petoe P, Poulsen AD, Prance GT, Quakenbush JP, Raes N, Rodda M, Rogers ZS, Schuiteman A, Schwartsburd P, P Scotland RW, Simmons MP, Simpson DA, Stevens P, Sundue M, Testo W, Trias-Blasi A, Turner I, Utteridge T, Walsingham L, Webber BL, Wei R, Weiblen GD, Weigend M, Weston P, de Wilde W, Wilkie P, Wilmot-Dear CM, Wilson HP, Wood JRI, Li-Bing Z, van Welzen PC. 2020. New Guinea has the world's richest island. Nature 1-5.

Carreño-Rocabado G, Peña-ClaroM, Bongers F, Alarcón A, Licona JC, Poorter L. 2012. Effects of disturbance intensity on species and functional diversity in a tropical forest. J Ecol 100 (6): 1453-1463.

Castilla, Antonio R, Pope N, Jha S. 2016. Positive density-dependent reproduction regulated by local Kinship and size in an understorey tropical tree. Ann Bot 117 (2): 319-329.

Chazdon RL. 2003. Tropical forest recovery: Legacies of human impact and natural disturbances. Perspect Plant Ecol Evol Syst 6 (1-2): 51-71.

Cirimwam, L, Doumenge C, Kahindo JM, Amani C. 2019. The effect of elevation on species richness in tropical forests depends on the considered lifeform: Results from an East African Mountain Forest. Trop Ecol 60 (4): 473-484.

Dezzotti A, Mortoro A, Medina A, Sbrancia R, Beltrán HA. 2019. Plant richness and life form diversity along vegetation and forest use gradients in Northwestern Patagonia of Argentina. Cerne 25 (3): 301-313.

Farneda FZ, Rocha R, López-Baucells A, Sampaio EM, Palmeirim JM, Bobrowiec PED, Grelle CEV, Meyer CFJ. 2018. Functional recovery of Amazonian bat assemblages following secondary forest succession. Biol Conserv 218: 192-199.

Fatem, Marten S, Djitmau DA, Ungirwalu A, Wanma OA, 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 (8): 3596-3605.

Fernández-Lugo S, De Nascimento L, Méndez J, González-Delgado G, Gomes EPC, Otto R, Arévalo JR, Fernández-Palacios JM. 2015. Seedling survival patterns in Macaronesian laurel forest: A long-term study in Tenerife (Canary Islands). Forestry 88 (1): 121-130.

Givnish TJ. 1999. On the causes of gradients in tropical tree diversity. J Ecol 87 (2): 193-210.

Goodale UM, Ashton MS, Berlyn GP, Gregoire TG, Singhakumara BMP, Tennakoon KU. 2012. Disturbance and tropical pioneer species: Patterns of association across life-history stages. For Ecol Manag 277: 54-66.

Gustafsson, Malin, Gustafsson L, Alloysius D, Falck J, Yap S, Karlsson A, Ilstedt U. 2016. Life-history traits predict the response to increased light among 33 tropical rainforest tree species. For Ecol Manag 362: 20-28.

Houter NC, Pons TL. 2014. Gap effects on leaf traits of tropical rainforest trees differing in juvenile light requirement. Oecologia 175 (1): 37-50.

Hunter, Maria O, Keller M, Morton D, Cook B, Lefsky M, Ducey M, Saleska S, De Oliveira RS, Schietti J, Zang R. 2015. Structural dynamics of tropical moist forest gaps. PLoS ONE 10 (7): 1-19. DOI: 10.1371/journal.pone.0132144

Itoh, Akira, Yamakura T, Ogino K, Lee HS, Ashton PS. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak, Malaysia. Plant Ecol 132 (2): 121-136.

Johnson, Daniel J, 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 (1869): 20172210. DOI: 10.1098/rspb.2017.2210.

Kartikasari SN, Marshall AJ, Beehler B. 2012. Ekologi Papua. Seri Ekologi Indonesia, Jilid VI. Yayasan Obor Indonesia dan Conservation International, Jakarta. [Indonesian]

Laurans M, Hérault B, Vieilledent G, Vincent G. 2014. Vertical stratification reduces competition for light in dense tropical forests. For Ecol Manag 329: 79-88.

Legendre, Pierre, Fortin MJ. 1989. Spatial pattern and ecological analysis. Vegetatio 80 (2): 107-138.

Liu JJ, Slik JWF. 2014. Forest fragment spatial distribution matters for tropical tree conservation. Biol Conserv 171: 99-106.

Lü XT, Tang JW. 2010. Structure and composition of the understory treelets in a non-dipterocarp forest of tropical Asia. For Ecol Manag 260 (4): 565-572.

Magrach, Ainhoa, Rodríguez-Pérez J, Campbell M, Laurance WF. 2014. Edge effects shape the spatial distribution of lianas and epiphytic ferns in Australian tropical rain forest fragments. Appl Veg Sci 17 (4): 754-764.

Menezes GSC, Cazetta E, Dodonov P. 2019. Vegetation structure across fire edges in a neotropical rain forest. For Ecol Manag 453:117587.

Montesinos-Navarro A, Estrada A, Font X, Matias MG, Meireles C, Mendoza M, Honrado JP, Prasad HD, Vicente JR, Early R. 2018. Community structure informs species geographic distributions. PLoS One 13 (5): 1-16. DOI: 10.1371/journal.pone.0197877

Montgomery RA, Chazdon RL. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82 (10): 2707-2718.

Murdjoko, Agustinus, 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(1): 33-47.

Murdjoko, Agustinus, Marsono D, Sadono R, Hadisusanto S. 2016b. Tree association with Pometia and its structure in logging concession of South Papua forest. Jurnal Manajemen Hutan Tropika (Journal of Tropical Forest Management) 22 (3): 180-191. [Indonesian]

Murdjoko, Agustinus, 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 (3): 230-245.

Oksane, J, Roeland KF, Blanchet G, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Wagner HM, Stevens HH. 2019. Package 'Vegan.' R Package Version 3.4.0.

Padmanaba M, Corlett RT. 2014. Minimizing risks of invasive alien plant species in tropical production forest management. Forests 5 (8): 1982-1998.

Pan, Yude, Birdsey RA, Phillips OL, Jackson RB. 2013. The structure, distribution, and biomass of the world's forests. Ann Rev Ecol Evol Syst 44 (1): 593-622.

Piotto D, Craven D, Montagnini F, Ashton M, Oliver C, Thomas WW. 2019. Successional, spatial, and seasonal changes in seed rain in the Atlantic forest of Southern Bahia, Brazil. PLoS ONE 14 (12): 1-15. DOI: 10.1371/journal.pone.0226474

Rahman MM, Tsukamoto J. 2015. Opposing effects of substrate quality and site factors on forest floor turnover rates: An example from the tropics. Forestry 88 (2): 190-199.

Robiansyah I. 2018. Diversity and biomass of tree species in Tambrauw, West Papua, Indonesia. Biodiversitas 19 (2): 377-386.

Rüger N, Berger U, Hubbell SP, Vieilledent G, Condit R. 2011. Growth strategies of tropical tree species: Disentangling light and size effects. PLoS ONE 6 (9): e25330. DOI: 10.1371/journal.pone.0025330

Sawada Yoshimi, Shin-ichiro A, Takyu M, Repin R, Nais J, Kitayama K,. 2015. Community dynamics over 14 years along gradients of geological substrate. J Trop Ecol 31 (2): 117-128.

Sebbenn AM, Degen B, Azevedo VCR, Silva MB, de Lacerda AEB, Ciampi AY, Kanashiro M, da S. Carneiro F, Thompson I, Loveless. 2008 MD. Modelling the long-term impacts of selective logging on genetic diversity and demographic structure of four tropical tree species in the Amazon forest. For Ecol Manag 254 (2): 335-349.

Seidler TG, Plotkin JB. 2006. Seed dispersal and spatial pattern in tropical trees. PLoS Biol 4 (11): e344. DOI: 10.1371/journal.pbio.0040344.

Slik JWF, Arroyo-Rodríguez V, Aiba SI, Alvarez-Loayza P, Alves LF, Ashton P, Balvanera P, Bastian ML, Bellingham PJ, Van Den Berg E, Bernacci L, Da Conceição Bispo P, Blanc L, Böhning-Gaese K, Boeckx P, Bongers F, Boyle B, Bradford M, Brearley FQ, Hockemba MBN, Bunyavejchewin S, Matos DCL, Castillo-Santiago M, Catharino ELM, Chai SL, Chen Y, Colwell RK, Robin CL, Clark C, Clark DB, Clark DA, Culmsee H, Damas K, Dattaraja HS, Dauby G, Davidar P, DeWalt SJ, Doucet JL, Duque A, Durigan G, Eichhorn KAO, Eisenlohr PV, Eler E, Ewango C, Farwig N, Feeley KJ, Ferreira L, Field R, De Oliveira Filho AT, Fletcher C, Forshed O, Franco G, Fredriksson G, Gillespie T, Gillet JF, Amarnath G, Griffith DM, Grogan J, Gunatilleke N, Harris D, Harrison R, Hector A, Homeier J, Imai N, Itoh A, Jansen PA, Joly CA, De Jong BHJ, Kartawinata K, Kearsley E, Kelly DL, Kenfack D, Kessler M, Kitayama K, Kooyman R, Larney E, Laumonier Y, Laurance S, Laurance WF, Lawes MJ, Do Amaral IL, Letche SG, Lindsell J, Lu X, Mansor A, Marjokorpi A, Martin EH, Meilby H, Melo FPL, Metcalfe DJ, Medjibe VP, Metzger JP, Millet J, Mohandass D, Montero JC, De Morisson Valeriano M, Mugerwa B, Nagamasu H, Nilus R, Ochoa-Gaona S, Onrizal, Page P, Parolin P, Parren M, Parthasarathy N, Paudel E, Permana A, Piedade MTF, Pitman NCA, Poorter L, Poulsen AD, Poulsen J, Powers J, Prasad RC, Puyravaud JP, Razafimahaimodison JC, Reitsma J, Dos Santos JR, Spironello WR, Romero-Saltos H, Rovero F, Rozak AH, Ruokolainen K, Rutishauser E, Saiter F, Saner P, Santos BA, Santos F, Sarker SK, Satdichanh M, Schmitt CB, Schöngart J, Schulze M, Suganuma MS, Sheil D, Da Silva Pinheiro E, Sist P, Stevart T, Sukumar R, Sun IF, Sunderand T, Suresh HS, Suzuki E, Tabarelli M, Tang J, Targhetta N, Theilade I, Thomas DW, Tchouto P, Hurtado J, Valencia R, Van Valkenburg JLCH, Van Do T, Vasquez R, Verbeeck H, Adekunle V, Vieira SA, Webb CO, Whitfeld T, Wich SA, Williams J, Wittmann F, Wöll H, Yang X, Yao CYA, Yap SL, Yoneda T, Zahawi RA, Zakaria R, Zang R, De Assis RL, Luize BG, Venticinque EM. 2015. An estimate of the number of tropical tree species. Proc Nat Acad Sci USA 112 (24): 7472-7477.

Slik JWF, Franklin J, Arroyo-Rodríguez V, Field R, Aguilar S, Aguirre N, Ahumada J, Aiba SI, Alves LF, Anitha K, Avella A, Mora F, Aymard GAC, Báez S, Balvanera P, Bastian ML, Bastin JF, Bellingham PJ, Van Den Berg E, Da Conceição Bispo P, Boeckx P, Boehning-Gaese K, Bongers F, Boyle F, Brambach F, Brearley FQ, Brown S, Chai SL, Chazdon RL, Chen S, Chhang P, Chuyong G, Ewango C, Coronado IM, Cristóbal-Azkarate J, Culmsee H, Damas K, Dattaraja HS, Davidar P, DeWalt SJ, Din H, Drake DR, Duque A, Durigan G, Eichhorn K, Eler ES, Enoki T, Ensslin A, Fandohan AB, Farwig N, Feeley KJ, Fischer M, Forshed O, Garcia QS, Garkoti SC, Gillespie TW, Gillet JF, Gonmadje C, Granzow-De La Cerda I, Griffith DM, Grogan J, Hakeem KR, Harris DJ, Harrison RD, Hector A, Andreas Hemp, Jürgen Homeier, M. Shah Hussain, Guillermo Ibarra-Manríquez, I. Faridah Hanum, Nobuo Imai, Jansen PA, Joly CA, Joseph S, Kartawinata K, Kearsley E, Kelly DL, Kessler M, Killeen TJ, Kooyman RM, Laumonier Y, Laurance SG, Laurance WF, Lawes MJ, Letcher SG, Lindsell J, Lovett J, Lozada J, Lu X, Lykke AM, Bin Mahmud K, Mahayani NPD, Mansor A, Marshall AR, Martin EH, Matos DCL, Meave JA, Melo FPL, Mendoza ZHM, Metali M, Medjibe VP, Metzger JP, Metzker T, Mohandass D, Munguía-Rosas MA, Muñoz R, Nurtjahya E, Eddie Lenza De Oliveira, Onrizal, Pia Parolin, Marc Parren, N. Parthasarathy, Ekananda Paudel, Rolando Perez, Pérez-García EA, Pommer U, Poorter L, Qi L, Piedade MTF, Pinto JRR, Poulsen AD, Poulsen JR, Powers JS, Prasad RC, Puyravaud JP, Rangel O, Reitsma J, Rocha DSB, Rolim S, Rovero F, Rozak A, Ruokolainen K, Rutishauser E, Rutten G, Said MNM, Saiter FZ, Saner P, Santos B, Dos Santos JR, Sarker SK, Schmitt CB, Schoengart J, Schulze M, Sheil D, Sist P, Souza AF, Spironello WR, Sposito T, Steinmetz R, Stevart T, Suganuma MS, Sukri R, Sultana A, Sukumar R, Sunderland T, Supriyadi, Suresh HS, Suzuki E, Tabarelli M, Tang J, Tanner EVJ, Targhetta N, Theilade I, Thomas D, Timberlake J, De Morisson Valeriano M, Van Valkenburg J, Van Do T, Van Sam H, Vandermeer JH, Verbeeck H, Vetaas OR, Adekunle V, Vieira SA, Webb CO, Webb EL, Whitfeld T, Wich S, Williams J, Wiser S, Wittmann F, Yang X, Yao CYA, Yap SL, Zahawi RA, Zakaria R, Zang R. 2018. Phylogenetic classification of the world's tropical forests. Proc Nat Acad Sci USA 115 (8): 1837-1842.

Steege HT, Henkel TW, Helal N, Marimon BS, Marimon-Junior BN, Huth A, Groeneveld J, Sabatier D, de Souza Coelho L, de Andrade LFD, Salomão RP, Amaral IL, de Almeida MFD, Castilho CV, Phillips OL, Guevara JE, de Jesus VCM, López DC, Magnusson WE, Wittmann F, Irume MV, Martins MP, da Silva GSR, Molino JF, Bánki OS, Piedade MTF, Pitman NCA, Mendoza AM, Ramos JF, Luize BG, de Leão NEMM, Vargas PN, Silva TSF, Venticinque EM, Manzatto AG, Reis NFC, Terborgh J, Casula KR, Coronado ENH, Montero JC, Feldpausch TR, Duque A, Costa FRC, Arboleda NC, Schöngart J, Killeen TJ, Vasquez R, Mostacedo B, Demarchi LO, Assis RL, Baraloto C, Engel J, Petronelli P, Castellanos P, de Medeiros MB, Quaresma A, Simon MF, Andrade A, Camargo JL, Laurance SGW, Laurance WF, Rincón LM, Schietti J, Sousa TR, de Sousa FE, Lopes MA, Magalhães JLL, Nascimento HEM, de Queiroz HL, Aymard CGA, Brienen R, Revilla JDC, Vieira ICG, Cintra BBL, Stevenson PR, Feitosa YO, Duivenvoorden JF, Mogollón HF, Araujo-Murakami A, Ferreira LV, Lozada JR, Comiskey JA, de Toledo JJ, Damasco G, Dávila N, Draper F, García-Villacorta R, Lopes A, Vicentini A, Alonso A, Dallmeier F, Gomes VHF, Lloyd J, Neill D, de Aguiar DPP, Arroyo L, Carvalho FA, de Souza FC, do Amaral DD, Feeley KJ, Gribel R, Pansonato MP, Barlow J, Berenguer E, Ferreira J, Fine PVA, Guedes MCA, Jimenez EM, Licona JC, Mora MCP, Villa B, Cerón C, Maas P, Silveira M, Stropp J, Thomas R, Baker TR, Daly D, Dexter KG, Huamantupa-Chuquimaco I, Milliken W, Pennington T, Paredes MR, Fuentes A, Klitgaard B, Pena JJM, Peres CA, Silman MR, Tello JS, Chave J, Valverde FC, Di Fiore A, Hilário RR, Phillips JF, Rivas-Torres G, van Andel TR, von Hildebrand P, Noronha JC, Barbosa EM, Barbosa FR, de Matos BLC, de Sá Carpanedo R, Doza HPD, Fonty E, Zárate RG, Gonzales T, Gonzales GPG, Hoffman B, Junqueira AB, Malhi Y, de Andrade MIP, Pinto LFM, Prieto A, de Jesus RD, Rudas A, Ruschel AR, Silva N, Vela CIA, Vos VA, Zent EL, Zent S, Albuquerque BW, Cano A, Márquez YAC, Correa DF, Costa JBP, Flores BM, Galbraith D, Holmgren M, Kalamandeen M, Nascimento MT, Oliveira AA, Ramirez-Angulo H, Rocha M, Scudeller VV, Sierra R, Tirado M, Medina MNU, van der Heijden G, Torre EV, Vriesendorp C, Wang O, Young KR, Reategui MAA, Baider C, Balslev H, Cárdenas S, Casas LF, Farfan-Rios W, Ferreira C, Linares-Palomino R, Mendoza C, Mesones I, Torres-Lezama A, Giraldo LEU, Villarroel D, Zagt R, Alexiades MN, de Oliveira EA, Garcia-Cabrera K, Hernandez L, Cuenca WP, Pansini S, Pauletto D, Arevalo FR, Sampaio AF, Sandoval EHV, Gamarra LV, Levesley A, Pickavance G, Melgaço K. 2019. Rarity of monodominance in hyperdiverse Amazonian Forests. Sci Rep 9 (1): 1-15.

Swaine MD, Lieberman D, Putz FE. 1987. The dynamics of tree populations in tronical forest: A review. J Trop Ecol 3 (4): 359-366.

Ter Braak CJF. 1986. Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. Ecology 67 (5): 1167-1179.

Thomas SC, Baltzer JL. 2002. Tropical Forests. Encyclopedia of Life Sciences 1-8.

Vergara-Rodrígue D, Mathieu G, Samain MS, Armenta-Montero S, Krömer T. 2017. Diversity, distribution, and conservation status of Peperomia (Piperaceae) in the State of Veracruz, Mexico. Trop Conserv Sci 10 (44): 1-18.

Vitousek, Peter M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65 (1): 285-298.

Wang, Hongxiang, Peng H, Hui G, Hu Y, Zhao Z. 2018. Large trees are surrounded by more heterospecific neighboring trees in Korean pine broad-leaved natural forests. Sci Rep 8 (1): 1-11.

Wright SJ, Muller-Landau HC. 2006. The uncertain future of tropical forest species. Biotropica 38 (4): 443-445.

Yamamoto, Shin-Ichi. 2000. Forest gap dynamics and tree regeneration. J For Res 5 (4): 223-229.

Zhu, Yan, Comita LS, Hubbell SP, Keping Ma. 2015. Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. J Ecol 103 (4): 957-966.

Table S1. Species name of heterospecific associations for understory for Figure 2

No.	Code	Species	Group 1	Group 2	Group 3
1	Kiba_co	*Kibara coriacea* (Blume) Hook. f. & A. Thomps.	+		
2	Rhus_la	*Rhus lamprocarpa* Merr. & L.M.Perry	+		
3	Dios_pi	*Diospyros pilosanthera* Blanco	+		
4	Lits_le	*Litsea ledermannii* Teschner	+		
5	Maca_gi	*Macaranga gigantea* (Rchb.f. & Zoll.) Müll.Arg.	+		
6	Maca_ta	*Macaranga tanarius* (L.) Müll.Arg.	+		
7	Seme_pa	*Semecarpus papuana* Lauterb.	+		
8	Ster_sh	*Sterculia shillinglawii* F.Muell.	+		
9	Case_ca	*Casearia carrii* Sleumer	+		
10	Xant_no	*Wendlandia* sp	+		
11	Teij_bo	*Teijsmanniodendron bogoriense* Koord.	+		
12	Flin_pi	*Flindersia pimenteliana* F.Muell.	+		
13	Case_sp	*Casearia* sp	+		
14	Hapl_ce	*Haplolobus celebicus* H.J.Lam	+		
15	Myri_en	*Myristica ensifolia* J.Sinclair	+		
16	Octa_in	*Octamyrtus insignis* Diels	+		
17	Piso_lo	*Pisonia longirostris* Teijsm. & Binn.	+		
18	Wend_sp	*Wendlandia* sp	+		
19	Timo_ca	*Timonius carii* S.P.Darwin	+		
20	Prun_ja	*Prunus javanica* (Teijsm. & Binn.) Miq.	+		
21	Hapl_fl	*Haplolobus floribundus* (K.Schum.) H.J.Lam	+		
22	Anti_de	*Alstonia spectabilis* R.Br.	+		
23	Buch_ar	*Buchanania arborescens* (Blume) Blume	+		
24	Cryp_pa	*Cryptocarya palmerensis* C.K.Allen	+		
25	Gmel_se	*Gmelina sessilis* C.T.White & W.D.Francis ex Lane-Poole	+		
26	Garc_pi	*Garcinia picrorhiza* Miq.	+		
27	Para_ve	*Parastemon versteeghii* Merr. & L.M.Perry	+		
28	Knem_in	*Knema intermedia* Warb.	+		
29	Case_mo	*Casearia monticola* Sleumer	+		
30	Half_ke	*Halfordia kendack* Guillaumin	+		
31	Syzy_ve	*Syzygium versteegii* (Lauterb.) Merr. & L.M.Perry	+		
32	Ficu_ro	*Ficus robusta* Corner	+		
33	Heri_sy	*Heritiera sylvatica* S.Vidal	+		
34	Cerb_fl	*Cerbera floribunda* K.Schum.	+		
35	Myri_gl	*Myristica globosa* Warb.	+		
36	Dryp_gl	*Drypetes globosa* (Merr.) Pax & K.Hoffm.	+		
37	Phal_ma	*Phaleria macrocarpa* (Scheff.) Boerl.	+		
38	Cana_ri	*Canarium rigidum* (Blume) Zipp. ex Miq.	+		
39	Lits_ti	*Litsea timoriana* Span.	+		
40	Timo_ti	*Timonius timon* (Spreng.) Merr.	+		
41	Homa_fo	*Heritiera sylvatica* S.Vidal	+		
42	Endo_me	*Endospermum medullosum* L.S.Sm.	+		
43	Pome_pi	*Pometia pinnata* J.R.Forst. & G.Forst.	+		
44	Kiba_bu	*Kibara bullata* Philipson	+		
45	Drac_da	*Dracontomelon dao* (Blanco) Merr. & Rolfe	+		
46	Goni_gi	*Goniothalamus giganteus* Hook.f. & Thomson	+		
47	Nauc_or	*Nauclea orientalis* (L.) L.	+		
48	Beil_mo	*Beilschmiedia morobensis* Kosterm.	+		
49	Cara_br	*Carallia brachiata* (Lour.) Merr.	+		
50	Lits_sp	*Litsea* sp	+		
51	Pime_am	*Pimelodendron amboinicum* Hassk.	+		
52	Medu_la	*Medusanthera laxiflora* (Miers) R.A.Howard	+		
53	Myri_fa	*Myristica fatua* Houtt.	+		
54	Gono_li	*Gonocaryum litorale* (Blume) Sleumer	+		
55	Lith_ru	*Lithocarpus rufovillosus* (Markgr.) Rehder	+		
56	Hope_pa	*Hopea papuana* Diels	+		
57	Dill_pa	*Dillenia papuana* Martelli	+		
58	Mast_pa	*Mastixiodendron pachyclados* (K.Schum.) Melch.	+		
59	Pome_ac	*Pometia acuminata* Radlk.	+		
60	Kiba_el	*Kibara elongata* A.C.Sm.	+		
61	Clei_pa	*Cleistanthus papuanus* (Lauterb.) Jabl.	+		
62	Ints_pa	*Intsia palembanica* Miq.	+		
63	Galb_be	*Galbulimima belgraveana* (F.Muell.) Sprague	+		

64	Term_co	*Terminalia copelandi* Elmer	+		
65	Giro_ne	*Gironniera nervosa* Planch.	+		
66	Mani_pl	*Maniltoa plurijuga* Merr. & L.M.Perry	+		
67	Hope_ce	*Hopea celtidifolia* Kosterm.	+		
68	Meli_el	*Melicope elleryana* (F. Muell.) T.G. Hartley	+		
69	Garc_sp	*Garcinia* sp	+		
70	Pala_lo	*Palaquium lobbianum* Burck	+		
71	Camp_br	*Campnosperma brevipetiolatum* Volkens	+		
72	Ster_ma	*Sterculia macrophylla* Vent.	+		
73	Harp_ca	*Harpullia carrii* Leenh.	+		
74	Hors_la	*Horsfieldia laevigata* Warb.	+		
75	Arch_pa	*Archidendron parviflorum* Pulle	+		
76	Chry_pa	*Chrysophyllum* papuanicum (Pierre ex Dubard) Royen	+		
77	Fagr_ra	*Fagraea racemosa* Jack	+		
78	Klei_ho	*Kleinhovia hospita* L.	+		
79	Endi_ru	*Endiandra rubescens* (Blume) Miq.	+		
80	Tris_ma	*Tristaniopsis macrosperma* (F.Muell.) Peter G.Wilson & J.T.Waterh.	+		
81	Cory_la	*Corynocarpus laevigatus* J.R.Forst. & G.Forst.	+		
82	Cryp_sp	*Cryptocarya* sp	+		
83	Tabe_au	*Tabernaemontana aurantiaca* Gaudich.	+		
84	Mall_sp	*Mallotus* sp	+		
85	Deca_pa	*Decaspermum* parviflorum (Lam.) A.J.Scott	+		
86	Agla_sp	*Aglaia spectabilis* (Miq.) S.S.Jain & S.Bennet	+		
87	Rapa_te	*Rapanea tempanpan* P.Royen	+		
88	Calo_ca	*Calophyllum caudatum* Kaneh. & Hatus.	+		
89	Xant_pa	*Xanthophyllum papuanum* Whitmore ex Meijden	+		
90	Hapl_la	*Haplolobus lanceolatus* H.J.Lam ex Leenh.	+		
91	Alst_sp	*Alstonia spectabilis* R.Br.			+
92	Dios_sp	*Diospyros* sp			+
93	Elae_an	*Elaeocarpus angustifolius* Blume			+
94	Rypa_ja	*Ryparosa javanica* Koord. & Valeton			+
95	Rhod_ci	*Rhodamnia cinerea* Jack			+
96	Myri_gi	*Myristica gigantea* King			+
97	Anti_to	*Antiaris toxicaria* Lesch.			+
98	Calo_in	*Calophyllum inophyllum* L.			+
99	Para_pr	*Pararchidendron pruinosum* (Benth.) I.C.Nielsen			+
100	Siph_ce	*Siphonodon celastrineus* Griff.			+
101	Siph_sp	*Siphonodon* sp			+
102	Maas_gl	*Maasia glauca* (Hassk.) Mols, Kessler & Rogstad			+
103	Term_ka	*Terminalia kaernbacchii* Warb.			+
104	Spat_ja	*Spathiostemon javensis* Blume		+	
105	Dyso_mo	*Dysoxylum mollissimum* Blume		+	
106	Plan_ke	*Planchonella keyensis* H.J.Lam		+	
107	Ficu_sp	*Ficus* sp		+	
108	Hors_pa	*Horsfieldia parviflora* (Roxb.) J.Sinclair		+	

Table S2. Species name of heterospecific associations for upper story Figure 3

No.	Code	Species	Group 1	Group 2	Group 3	Group 4
1	Hors_ir	*Horsfieldia irya* (Gaertn.) Warb.		+		
2	Garc_la	*Garcinia latissima* Miq.		+		
3	Alst_sc	*Alstonia scholaris* (L.) R. Br.		+		
4	Endi_vi	*Endiandra virens* F.Muell.		+		
5	Sloa_pu	*Sloanea pullei* O.C.Schmidt ex A.C.Sm.		+		
6	Galb_be	*Galbulimima belgraveana* (F.Muell.) Sprague		+		
7	Pome_ac	*Pometia acuminata* Radlk.		+		
8	Chis_ce	*Chisocheton ceramicus* Miq.		+		
9	Dyso_mo	*Dysoxylum mollissimum* Blume		+		
10	Endo_me	*Endospermum medullosum* L.S.Sm.		+		
11	Pime_am	*Pimelodendron amboinicum* Hassk.		+		
12	Gono_li	*Gonocaryum littorale* (Blume) Sleumer	+			
13	Stre_el	*Streblus elongatus* (Miq.) Corner	+			
14	Homa_fo	*Heritiera sylvatica* S.Vidal	+			
15	Gnet_gn	*Gnetum gnemon* L.	+			
16	Homa_no	*Homalanthus novoguineensis* (Warb.) K.Schum.	+			
17	Cory_la	*Corynocarpus laevigatus* J.R.Forst. & G.Forst.	+			
18	Drac_da	*Dracontomelon dao* (Blanco) Merr. & Rolfe	+			
19	Cana_od	*Canarium indicum* L.	+			
20	Pter_be	*Pterocymbium beccarii* K.Schum.	+			
21	Pala_lo	*Palaquium lobbianum* Burck	+			
22	Cana_in	*Canarium indicum* L.	+			
23	Cara_br	*Carallia brachiata* (Lour.) Merr.	+			
24	Timo_ca	*Timonius carii* S.P.Darwin	+			
25	Hors_sy	*Horsfieldia sylvestris* Warb.	+			
26	Maas_su	*Maasia sumatrana* (Miq.) Mols, Kessler & Rogstad	+			
27	Hope_pa	*Hopea papuana* Diels	+			
28	Hope_ce	*Hopea celtidifolia* Kosterm.	+			
29	Rhus_ta	*Rhus taitensis* Guill.	+			
30	Acti_ni	*Actinodaphne nitida* Teschner	+			
31	Dill_pa	*Dillenia papuana* Martelli	+			
32	Medu_la	*Medusanthera laxiflora* (Miers) R.A.Howard	+			
33	Teij_bo	*Teijsmanniodendron bogoriense* Koord.	+			
34	Tris_ma	*Tristaniopsis macrosperma* (F.Muell.) Peter G.Wilson & J.T.Waterh.	+			
35	Call_lo	*Callicarpa longifolia* Lam.	+			
36	Comm_ba	*Commersonia bartramia* (L.) Merr.	+			
37	Dios_pi	*Diospyros pilosanthera* Blanco	+			
38	Knem_in	*Knema intermedia* Warb.	+			
39	Dryp_gl	*Drypetes globosa* (Merr.) Pax & K.Hoffm.	+			
40	Cryp_pa	*Cryptocarya palmerensis* C.K.Allen	+			
41	Meli_el	*Melicope elleryana* (F. Muell.) T.G. Hartley	+			
42	Lits_ti	*Litsea timoriana* Span.	+			
43	Siph_ce	*Siphonodon* celastrineus Griff.	+			
44	Siph_sp	*Siphonodon* sp	+			
45	Vite_pi	*Vitex pinnata* L.	+			
46	Poly_no	*Polyscias nodosa* (Blume) Seem.	+			
47	Pome_pi	*Pometia pinnata* J.R.Forst. & G.Forst.	+			
48	Agla_ar	*Aglaia argentea* Blume	+			
49	Acro_sp	*Acronychia* sp	+			
50	Gmel_se	*Gmelina sessilis* C.T.White & W.D.Francis ex Lane-Poole	+			
51	Mani_br	*Maniltoa browneoides* Harms	+			
52	Prun_ar	*Prunus arborea* (Blume) Kalkman	+			
53	Camp_br	*Campnosperma brevipetiolatum* Volkens	+			
54	Hors_la	*Horsfieldia laevigata* Warb.	+			
55	Cana_hi	*Campnosperma brevipetiolatum* Volkens	+			
56	Deca_pa	*Decaspermum parviflorum* (Lam.) A.J.Scott	+			
57	Calo_in	*Calophyllum inophyllum* L.	+			
58	Heri_sy	*Heritiera sylvatica* S.Vidal	+			
59	Clei_pa	*Cleistanthus papuanus* (Lauterb.) Jabl.	+			
60	Elae_an	*Elaeocarpus angustifolius* Blume	+			
61	Gymn_fa	*Gymnacranthera farquhariana* (Hook.f. & Thomson) Warb.	+			
62	Grew_er	*Grewia eriocarpa* Juss.	+			
63	Xant_no	*Wendlandia* sp	+			

64	Rhod_ci	*Rhodamnia cinerea* Jack	+			
65	Arto_al	*Artocarpus altilis* (Parkinson ex F.A.Zorn) Fosberg	+			
66	Para_pr	*Pararchidendron pruinosum* (Benth.) I.C.Nielsen	+			
67	Plan_ke	*Planchonella keyensis* H.J.Lam	+			
68	Dios_pa	*Diospyros papuana* Valeton ex Bakh.	+			
69	Ochr_gl	*Ochrosia glomerata* (Blume) F.Muell.	+			
70	Myri_fa	*Myristica fatua* Houtt.	+			
71	Ster_sh	*Sterculia shillinglawii* F.Muell.	+			
72	Syzy_sp2	*Syzygium* sp2	+			
73	Syzy_sp3	*Syzygium* sp3	+			
74	Xant_pa	*Xanthophyllum* papuanum Whitmore ex Meijden	+			
75	Euca_pa	*Eucalyptopsis papuana* C.T.White			+	
76	Flin_pi	*Flindersia pimenteliana* F.Muell.			+	
77	Hapl_fl	*Haplolobus floribundus* (K.Schum.) H.J.Lam			+	
78	Lits_fi	*Litsea firma* (Blume) Hook.f.			+	
79	Term_co	*Terminalia copelandi* Elmer			+	
80	Calo_ca	*Calophyllum caudatum* Kaneh. & Hatus.			+	
81	Coch_gi	*Cochlospermum gillivraei* Benth.			+	
82	Buch_ar	*Buchanania arborescens* (Blume) Blume			+	
83	Fagr_el	*Fagraea elliptica* Roxb.				+
84	Prun_ja	*Prunus javanica* (Teijsm. & Binn.) Miq.				+
85	Endi_ru	*Endiandra rubescens* (Blume) Miq.				+
86	Cryp_sp	*Cryptocarya* sp				+

Table S3. Species name of conspecific associations Figure 4. The S stands for small individuals and L symbolizes large individuals.

No.	Code		Species
1	Agla_ar	_L	*Aglaia argentea* Blume
2	Agla_ar	_S	*Aglaia argentea* Blume
3	Buch_ar	_L	*Buchanania arborescens* (Blume) Blume
4	Buch_ar	_S	*Buchanania arborescens* (Blume) Blume
5	Calo_ca	_L	*Calophyllum caudatum* Kaneh. & Hatus.
6	Calo_ca	_S	*Calophyllum caudatum* Kaneh. & Hatus.
7	Calo_in	_L	*Calophyllum inophyllum* L.
8	Calo_in	_S	*Calophyllum inophyllum* L.
9	Camp_br	_L	*Campnosperma brevipetiolatum* Volkens
10	Camp_br	_S	*Campnosperma brevipetiolatum* Volkens
11	Cana_hi	_L	*Canarium hirsutum* Willd.
12	Cana_hi	_S	*Canarium hirsutum* Willd.
13	Cana_in	_L	*Canarium indicum* L.
14	Cana_in	_S	*Canarium indicum* L.
15	Cara_br	_L	*Carallia brachiata* (Lour.) Merr.
16	Cara_br	_S	*Carallia brachiata* (Lour.) Merr.
17	Clei_pa	_L	*Cleistanthus papuanus* (Lauterb.) Jabl.
18	Clei_pa	_S	*Cleistanthus papuanus* (Lauterb.) Jabl.
19	Cory_la	_L	*Corynocarpus laevigatus* J.R.Forst. & G.Forst.
20	Cory_la	_S	*Corynocarpus laevigatus* J.R.Forst. & G.Forst.
21	Cryp_pa	_L	*Cryptocarya palmerensis* C.K.Allen
22	Cryp_pa	_S	*Cryptocarya palmerensis* C.K.Allen
23	Cryp_sp	_L	*Cryptocarya* sp
24	Cryp_sp	_S	*Cryptocarya* sp
25	Deca_pa	_L	*Decaspermum parviflorum* (Lam.) A.J.Scott
26	Deca_pa	_S	*Decaspermum parviflorum* (Lam.) A.J.Scott
27	Dill_pa	_L	*Dillenia papuana* Martelli
28	Dill_pa	_S	*Dillenia papuana* Martelli
29	Dios_pi	_L	*Diospyros pilosanthera* Blanco
30	Dios_pi	_S	*Diospyros pilosanthera* Blanco
31	Drac_da	_L	*Dracontomelon dao* (Blanco) Merr. & Rolfe
32	Drac_da	_S	*Dracontomelon dao* (Blanco) Merr. & Rolfe
33	Dryp_gl	_L	*Drypetes globosa* (Merr.) Pax & K.Hoffm.
34	Dryp_gl	_S	*Drypetes globosa* (Merr.) Pax & K.Hoffm.
35	Dyso_mo	_L	*Dysoxylum mollissimum* Blume
36	Dyso_mo	_S	*Dysoxylum mollissimum* Blume
37	Elae_an	_L	*Elaeocarpus angustifolius* Blume
38	Elae_an	_S	*Elaeocarpus angustifolius* Blume
39	Endi_ru	_L	*Endiandra rubescens* (Blume) Miq.
40	Endi_ru	_S	*Endiandra rubescens* (Blume) Miq.
41	Endo_me	_L	*Endospermum medullosum* L.S.Sm.
42	Endo_me	_S	*Endospermum medullosum* L.S.Sm.
43	Flin_pi	_L	*Flindersia pimenteliana* F.Muell.
44	Flin_pi	_S	*Flindersia pimenteliana* F.Muell.
45	Galb_be	_L	*Galbulimima belgraveana* (F.Muell.) Sprague
46	Galb_be	_S	*Galbulimima belgraveana* (F.Muell.) Sprague
47	Garc_la	_L	*Garcinia latissima* Miq.
48	Garc_la	_S	*Garcinia latissima* Miq.
49	Giro_ne	_L	*Gironniera nervosa* Planch.
50	Giro_ne	_S	*Gironniera nervosa* Planch.
51	Gmel_se	_L	*Gmelina sessilis* C.T.White & W.D.Francis ex Lane-Poole
52	Gmel_se	_S	*Gmelina sessilis* C.T.White & W.D.Francis ex Lane-Poole
53	Gnet_gn	_L	*Gnetum gnemon* L.
54	Gnet_gn	_S	*Gnetum gnemon* L.
55	Gono_li	_L	*Gonocaryum littorale* (Blume) Sleumer
56	Gono_li	_S	*Gonocaryum littorale* (Blume) Sleumer
57	Gymn_fa	_L	*Gymnacranthera farquhariana* (Hook.f. & Thomson) Warb.
58	Gymn_fa	_S	*Gymnacranthera farquhariana* (Hook.f. & Thomson) Warb.
59	Hapl_fl	_L	*Haplolobus floribundus* (K.Schum.) H.J.Lam
60	Hapl_fl	_S	*Haplolobus floribundus* (K.Schum.) H.J.Lam
61	Heri_sy	_L	*Heritiera sylvatica* S.Vidal
62	Heri_sy	_S	*Heritiera sylvatica* S.Vidal
63	Homa_fo	_L	*Homalium foetidum* Benth.
64	Homa_fo	_S	*Homalium foetidum* Benth.
65	Hope_ce	_L	*Hopea celtidifolia* Kosterm.
66	Hope_ce	_S	*Hopea celtidifolia* Kosterm.
67	Hope_no	_L	*Hopea novoguineensis* Slooten

68	Hope_no	_S	*Hopea novoguineensis* Slooten
69	Hope_pa	_L	*Hopea papuana* Diels
70	Hope_pa	_S	*Hopea papuana* Diels
71	Hors_la	_L	*Horsfieldia laevigata* Warb.
72	Hors_la	_S	*Horsfieldia laevigata* Warb.
73	Ints_pa	_L	*Intsia palembanica* Miq.
74	Ints_pa	_S	*Intsia palembanica* Miq.
75	Knem_in	_L	*Knema intermedia* Warb.
76	Knem_in	_S	*Knema intermedia* Warb.
77	Lith_ru	_L	*Lithocarpus rufovillosus* (Markgr.) Rehder
78	Lith_ru	_S	*Lithocarpus rufovillosus* (Markgr.) Rehder
79	Lits_ti	_L	*Litsea timoriana* Span.
80	Lits_ti	_S	*Litsea timoriana* Span.
81	Mani_br	_L	*Maniltoa browneoides* Harms
82	Mani_br	_S	*Maniltoa browneoides* Harms
83	Medu_la	_L	*Medusanthera laxiflora* (Miers) R.A.Howard
84	Medu_la	_S	*Medusanthera laxiflora* (Miers) R.A.Howard
85	Meli_el	_L	*Melicope elleryana* (F. Muell.) T.G. Hartley
86	Meli_el	_S	*Melicope elleryana* (F. Muell.) T.G. Hartley
87	Myri_fa	_L	*Myristica fatua* Houtt.
88	Myri_fa	_S	*Myristica fatua* Houtt.
89	Pala_lo	_L	*Palaquium lobbianum* Burck
90	Pala_lo	_S	*Palaquium lobbianum* Burck
91	Para_pr	_L	*Pararchidendron pruinosum* (Benth.) I.C.Nielsen
92	Para_pr	_S	*Pararchidendron pruinosum* (Benth.) I.C.Nielsen
93	Para_ve	_L	*Parastemon versteeghii* Merr. & L.M.Perry
94	Para_ve	_S	*Parastemon versteeghii* Merr. & L.M.Perry
95	Pime_am	_L	*Pimelodendron amboinicum* Hassk.
96	Pime_am	_S	*Pimelodendron amboinicum* Hassk.
97	Plan_ke	_L	*Planchonella keyensis* H.J.Lam
98	Plan_ke	_S	*Planchonella keyensis* H.J.Lam
99	Pome_ac	_L	*Pometia acuminata* Radlk.
100	Pome_ac	_S	*Pometia acuminata* Radlk.
101	Pome_pi	_L	*Pometia pinnata* J.R.Forst. & G.Forst.
102	Pome_pi	_S	*Pometia pinnata* J.R.Forst. & G.Forst.
103	Prun_ar	_L	*Prunus arborea* (Blume) Kalkman
104	Prun_ar	_S	*Prunus arborea* (Blume) Kalkman
105	Prun_ja	_L	*Prunus javanica* (Teijsm. & Binn.) Miq.
106	Prun_ja	_S	*Prunus javanica* (Teijsm. & Binn.) Miq.
107	Rhod_ci	_L	*Rhodamnia cinerea* Jack
108	Rhod_ci	_S	*Rhodamnia cinerea* Jack
109	Siph_ce	_L	*Siphonodon celastrineus* Griff.
110	Siph_ce	_S	*Siphonodon celastrineus* Griff.
111	Siph_sp	_L	*Siphonodon* sp
112	Siph_sp	_S	*Siphonodon* sp
113	Sloa_pu	_L	*Sloanea pullei* O.C.Schmidt ex A.C.Sm.
114	Sloa_pu	_S	*Sloanea pullei* O.C.Schmidt ex A.C.Sm.
115	Ster_sh	_L	*Sterculia shillinglawii* F.Muell.
116	Ster_sh	_S	*Sterculia shillinglawii* F.Muell.
117	Syzy_sp1	_L	*Syzygium* sp1
118	Syzy_sp1	_S	*Syzygium* sp1
119	Teij_bo	_L	*Teijsmanniodendron bogoriense* Koord.
120	Teij_bo	_S	*Teijsmanniodendron bogoriense* Koord.
121	Term_co	_L	*Terminalia copelandi* Elmer
122	Term_co	_S	*Terminalia copelandi* Elmer
123	Timo_ca	_L	*Timonius carii* S.P.Darwin
124	Timo_ca	_S	*Timonius carii* S.P.Darwin
125	Tris_ma	_L	*Tristaniopsis macrosperma* (F.Muell.) Peter G.Wilson & J.T.Waterh.
126	Tris_ma	_S	*Tristaniopsis macrosperma* (F.Muell.) Peter G.Wilson & J.T.Waterh.
127	Vati_ra	_L	*Vatica rassak* Blume
128	Vati_ra	_S	*Vatica rassak* Blume
129	Xant_pa	_L	*Xanthophyllum papuanum* Whitmore ex Meijden
130	Xant_pa	_S	*Xanthophyllum papuanum* Whitmore ex Meijden
131	Xant_no	_L	*Xanthostemon novaguineensis* Valeton
132	Xant_no	_S	*Xanthostemon novaguineensis* Valeton

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