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Abstract
Many plants in New Guinean rainforest have relatively larger fruits than those in other tropical forests and may depend on large animal dispersers, but little is known about the impacts of forest disturbance, especially logging, on the species composition and abundance of these trees. In order to provide a baseline for the understanding of their vulnerability, we counted fruiting plants and measured habitat parameters in primary and human-altered habitats in the little studied lowland forest of northern Papua, Indonesia. During the surveys coinciding with peak fruit season, eighty-nine species were recorded in fruit, with 71 species in 24 families known to be consumed by birds, and most of them (97%) were trees. The diversity of bird-consumed fruiting plants differed among the habitat types and was highest in undisturbed primary forest and hunted primary forest. Secondary forests still had a high number of species and individuals but were dominated by light demanding plants and a low number of uniquely found species. Logged forest and agricultural habitats showed only a low abundance of bird-consumed fruiting plants, being about 2-3 times lower than in primary forests. Plants with large sized fruits (diam. > 20 mm) were mainly found in primary forests, confirming their importance for maintaining interactions between large frugivorous birds and plants that are of relevance for forest regeneration.

Keywords
cassowary, frugivores, fruiting trees, logging, lowland forest, Papua

Introduction
Anthropogenic forest disturbance is rapidly increasing in tropical forests of Indonesia, especially in the Papua region, one of the last tropical wilderness areas in the world. Rapid development and human population growth are among the main drivers of the high rates of deforestation and forest conversion in this region. Besides large-scale oil palm plantations (Frazier, 2007), disturbance from logging is a primary cause for the loss of lowland primary forest in Papua. In general, forest disturbance can change plant and animal populations because it alters abiotic conditions that influence the abundance and diversity of organisms (Johns, 1997; Saunders et al., 1991), and cause large scale tree mortality and destruction of undergrowth and soils (Moore & Allard, 2011). Furthermore, species composition within habitats and interactions between flora and fauna may be affected. A common result of human forest use is structural change to the canopy due to forest clearing or the creation of trails allowing more light to reach the forest floor (Lefevre, 2008). In tropical rainforests this may change the microclimate, creating hotter, drier and windier conditions, especially near forest edges (Frumhoff, 1995; Hardwick et al., 2015). Additionally, human-induced forest disturbance frequently leads to increased prevalence of common species with reduced overall species and genetic diversity (Alroy, 2017;...
Vellend, 2004) and a high frequency of early successional species (Drapeau et al., 2000; Meijaard et al., 2005). Many plants are particularly vulnerable to forest disturbance if they are involved in mutualistic interactions with animals that are themselves influenced by human disturbances (Lefevre, 2008; Wright, 2005). For example, the seed dispersal process is an important component of the life cycle of plants that can be altered by forest disturbance (Aquilar et al., 2006; Neuschulz et al., 2016), such as via the disappearance of seed dispersing animals.

Fruiting plants play important roles in the forest ecosystem because they can importantly contribute to the diet of many forest animals. Changes in the community patterns and abundance of food plants may therefore induce changes in animal communities (Costa & Magnusson, 2003; Johns, 1997; Meijaard et al., 2005), particularly for frugivores that are dependent on fruiting plants. The responses of frugivores to forest and habitat alteration are species specific (Marsden & Pilgrim, 2003), and are generally related to fruit availability and vegetation structure (e.g. Bentrupperbaumer, 1998; Wright, 2005). Some frugivorous birds like the northern cassowary *Casuarius unappendiculatus* and the Victoria crowned pigeon *Goura victoria* in Papua, and most hornbills in Sumatra and Sulawesi islands avoid habitats where fruit availability is low due to heavy forest exploitation such as through intensive logging (Anggraini et al., 2000; Keiluhu et al., 2019; Kinnaird & O’Brien, 2005; Pangau-Adam et al., 2015). However, partial frugivores like the Megapodes appear to be unaffected by logging operations (Pangau-Adam & Brodie, 2019). Regarding mammalian frugivores, Rosenbaum et al. (1998) found the population abundance of Sulawesi crested black macaques *Macaca nigra* being lower in logged forest than in primary forest because of insufficient food resources in the former habitat. It appears that habitats with high variety and abundance of fruiting plants may support healthy populations and a high diversity of frugivores.

Because of the significant ecological role of fruiting plants, and the ongoing rapid forest disturbance in lowlands of Papua (Fraser, 2018), it is particularly important to assess fruiting plant communities in this area. The aim of this study was to investigate the effects of forest disturbance on species diversity and the abundance of fruiting plants, especially those species which provide food for frugivorous birds. The coverage of plantations and illegally logged areas in Papua is increasing rapidly with accelerating regional development (Fraser, 2018; Keiluhu et al., 2019), and therefore, our data from 2014 are relevant in the context of managing Papua’s forest ecosystems.

**Methods**

**Study Sites**

The Nimbokrang and Nimboran forests are located in the northern part of Indonesian New Guinea, about 110-120 km west of Jayapura, the capital of Papua Province (Figure 1). The lowlands consist of a mosaic of forest habitats including large portions of intact forest. Although forests around the villages have been cleared for timber and agriculture, large primary forest areas still remain. The elevation of the study area ranges from 50 to 200 m above sea level, and the vegetation is humid (lowland) tropical rainforest subject to inundation (CI, 1999). The forest canopy is dominated by the tree genera *Instia*, *Terminalia*, *Pometia*, *Cryptocarya*, *Ficus*, *Canarium*, and *Alstonia* while understory trees include *Areceaceae*, *Microcos*, *Myristica*, *Syzygium*, *Garcinia*, *Diospyros*, and *Pandanus*. Significant areas of the forest are claimed as traditional or clan forest by the local people, and there are several land use systems including agricultures. Parts of the forest were selectively logged by timber companies during the 1980s.

**Habitat Structure and Surveys on Fruiting Plants**

Field survey was conducted in five habitat types based on preliminary field assessment. Undisturbed primary forest and four different habitat types across a gradient of disturbance were chosen. Disturbed habitats include hunted primary forest, i.e. primary forests visited occasionally by local people for wildlife hunting, >30 year old secondary forest, less than 3 year old selectively logged forest, and agricultural areas. The last category is a small-scale mix of plantations of different crops and abandoned logged forest as practiced by local people in forest areas. Major crops include cocoa *Theobroma cacao*, cassava *Manihot utilissima*, sweet potato *Ipomoea batatas*, taro *Colocasia esculenta*, betel nut *Areca catechu* and banana *Musa* spp. Surveys of fruiting plants were conducted in April to July 2014 coinciding with peak fruit diversity in New Guinea (Wright, 2005), using a standard transect walk. Twelve transects were established systematically in each of five habitats, resulting in a sample size of 60 transects across the whole study area. Transects were located at least 300 meters apart, and the length of each transect was 1.5 km. To quantify the fruiting plants, transects were walked slowly and scanned until a distance of ca. 7.5 m to each side. All plants having fruits greater than 1 cm in diameter that were in fruit at the time of the survey were counted. Plant identification was done with the aid of literature (Baker & Dransfield, 2006; Cooper, 2013; Womersley & Conn, 1978) and through consultation with botanists and foresters. A number of trees were identified in
Herbarium Manokwarienses Papua and Herbarium Naturalis Biodiversity Center Leiden using voucher specimens collected during the surveys. Additional information was gathered from personal communications with the local botanists, foresters and ornithologists as well as with Andrew Mack and Debra Wright (formerly working at the Wildlife Conservation Society) and Max van Balgooy (Herbarium Naturalis Leiden). We tried to identify all fruiting plants in all sites. However, some species were only identified to the genus level. Plant species whose fruits are not consumed by birds were excluded from statistical analysis.

Whether fruiting plants were eaten by birds was determined through observation in the field, by noting if birds were observed feeding on the fruit. Since not all fruiting plants were visited by frugivores during fieldwork, data on cassowary diet (Pangau-Adam et al., 2015) and literature searches (e.g. Beehler & Dumbacher, 1996; Brown & Hopkins, 2002; Coates & Peckover, 2001; Keiluhu, 2013; Pangau-Adam & Muehlenberg, 2014; Pratt & Stiles, 1985; Terborgh & Diamond, 1970) were useful for the identification of those fruiting species known as being bird-dispersed in the region.

**Data Analyses**

To analyse species diversity, we used two indices representing alpha diversity of fruiting plants (consumed by birds only) in different habitats. Simpson’s index determines species richness in each habitat studied (the number of species encountered) for fruiting plants. The Shannon-Wiener index \( H = - \sum p_i \ln p_i \) where \( p_i \) is the proportional abundance of species \( i \) takes into account both species richness and the relative abundance of each species (Magurran, 2004). Fruiting plant abundance was measured as the total number of individuals encountered per transect. The mean abundance of fruiting plants was calculated for each transect and the comparison between habitats was analysed using one-way ANOVA.

As a measure of forest disturbance, we counted the number of human trails intersecting each transect and measured the distance of the starting point of each transect to the nearest village. Some habitat parameters were measured and analysed at the transect level, with habitat as the grouping variable. The circular plot method was used to collect vegetation data. At least three 5-m radius plots were established 10 m from, and perpendicular to, either side of each transect. Within each plot, the diameter at breast height (DBH) was measured and the height of all trees having a DBH ≥10 cm was estimated. At the center of each plot, the percent canopy cover was estimated visually and the average calculated for each transect. Differences in vegetation parameters between habitats were tested using the Kruskal-Wallis test and \( p \)-values were adjusted using Bonferroni correction (Fahrmeir et al., 2010). We assessed bivariate relationships between fruiting tree abundance and

![Figure 1. Map of Nimbokrang and Nimboran Forests in Papua Province, Indonesia, and Study Area Showing Habitat Types Sampled and Locations of Transects.](image-url)
anthropogenic activities as well as vegetation variables using Spearman rank. All statistical analysis were run using the STATISTICA Program.

Results

Anthropogenic activities and vegetation structures. During the survey there was a low number of human trails found in the primary forest, intermediate numbers in hunted primary forest and secondary forest, and the highest number in logged forest and agriculture. All habitat variables differed significantly between habitat types (Table 1). Canopy cover, which was related to land use changes, declined with increasing forest disturbance in the study sites. Undisturbed primary forest had a significantly higher average canopy cover (71.67%), tree height (20.65 m) and tree diameter (31.1 cm), and significantly lower understory cover (40.0%), than the other habitats. Hunted primary forest had a high canopy cover (average = 68.7%), not being significantly different from that of undisturbed primary forest. Secondary forest showed intermediate values for vertical levels of vegetation cover, tree height and tree diameter. Logged forest had a lower average tree diameter, tree height and canopy cover, and agriculture had the smallest and shortest trees and the sparsest canopy cover (Table 1). The average distance of transects to the nearest village was significantly different between habitat types ($H = 26.67$, df = 4, n = 58, $p < 0.01$), ranging from an average of 3.87 km in agricultures to 11.8 km in undisturbed primary forest.

Species richness and diversity of fruiting plants. We recorded a total of 89 plant species that fruited during the surveys; 71 species (in 24 families) of these were consumed by birds and most of them (97%) were trees (Table 1 Supplement material). Most of these fruiting plants were eaten and dispersed by cassowaries (Pangau-Adam et al., 2015; pers. observation), yet other frugivorous birds like birds of paradise, parrots, hornbills, fruit pigeons, and brush turkeys also fed on some of these plants. The size of fruits (diameter) ranged from 10 mm of *Licuala lauterbachii* to 135 mm of *Pandanus tectorius* (Table 1 Supplement material), although the size of the whole fruit of *Borassus heineanus* is about 140 mm. The most frequently recorded families included Arecaceae (11 species) and Myrtaceae (9 spp.), followed by Moraceae (6 spp.) and Anacardiaceae, Clusiaceae, Combretaceae, and Pandanaceae (each with 4 species). Of all the fruiting plants consumed by birds, 25 species were found in fruit exclusively in a single habitat. Eleven species were recorded only in hunted primary forest, 8 and 2 species in primary and secondary forest, respectively, and 4 species in agriculture habitat of which two are cultivated trees: *Areca catechu* and *Psidium guajava*. These data may indicate the species that were most impacted by disturbance (Table 3). The Simpson’s index of diversity was similar in three habitat types, but considerably lower in logged forest and agriculture habitats (Table 2). Shannon diversity differed among the five habitats, being highest in hunted primary forest followed by undisturbed primary forest and secondary forest (Table 2). Logged forest had a low diversity value, and the lowest was in agriculture that had few species and a dominance of certain palm species such as *Actinorhysis calapparia* and *Areca catechu*. Hunted primary forest and secondary forest showed a greater evenness in species than the other habitats, whereas both undisturbed and hunted primary forests had a higher species richness than the others (Figure 2).

Fruiting tree abundance and habitat variables. The abundance of fruiting plants, measured as encounters per transect, was significantly different among habitat types ($F_{4,55} = 8.593$, $p < .001$). Mann-Whitney-U-Test shows the difference between habitats, i.e. undisturbed forest (UPF) and logged forest $U = 1743.00$, $Z = 3.46$, $p < .001$, UPF and agriculture $U = 1470.50$, $Z = 4.29$, $p < .001$, hunted primary forest (HPH) and logged forest $U = 1540.00$, $Z = 4.29$, $p < .001$, HPH and agriculture $U = 1254.50$, $Z = 5.67$, $p < .001$, secondary forest (SF) and logged forest $U = 1889.00$, $Z = 2.85$, $p < .001$ and SF and agriculture $U = 1608.50$, $Z = 4.26$, $p < .001$.

The mean number of fruiting plants was highest in undisturbed and hunted primary forest (12.5 ± 4.5 and 12.5 ± 3.5, respectively) followed by secondary forest

### Table 1. Averages and Standard Deviations (in Brackets) of Habitat and Anthropogenic Variables for Each of Five Studied Habitat Types, in Northern Papua, Indonesia.

| Variables                  | Undisturbed primary forest | Hunted primary forest | Secondary forest | Logged forest | Agriculture | Kruskal-Wallis P |
|----------------------------|----------------------------|-----------------------|-----------------|--------------|-------------|------------------|
| Canopy cover (%)           | 71.67 (6.64)               | 68.67 (6.47)          | 63.42 (5.07)    | 40.58 (9.76) | 24.58 (8.05) | <0.01            |
| Understorey cover (%)      | 40.0 (5.49)                | 43.92 (5.99)          | 51.58 (8.89)    | 60.83 (7.10) | 58.25 (5.17)  | <0.05            |
| Tree height (m)            | 20.65 (1.64)               | 17.33 (2.02)          | 16.29 (2.27)    | 11.8 (1.67)  | 8.28 (1.33)   | <0.01            |
| DBH (cm)                   | 31.1 (3.28)                | 27.56 (4.53)          | 23.63 (4.8)     | 16.79 (3.80) | 12.94 (2.59)  | <0.01            |
| Human trails               | 0.17 (0.39)                | 0.67 (0.65)           | 1.17 (0.71)     | 1.92 (0.67)  | 2.18 (0.83)   | <0.01            |

The results of the Kruskal-Wallis tests for differences between these values are also listed.
and lowest in logged forest and agriculture (Figure 3). Fruiting tree abundance strongly correlated with tree canopy cover and tree diameter ($r_s = 0.67$, $p < 0.05$ and $r_s = 0.61$, $p < 0.05$ respectively), and moderately so with the distance of transects to villages ($r_s = 0.50$, $p < 0.05$). Fruiting tree abundance was negatively correlated with human trails ($r_s = -0.52$, $p < 0.05$) and understory cover ($r_s = -0.36$, $p < 0.05$).

### Discussion

Our study provides the first assessment of fruiting plants in the lowland forests of Indonesian New Guinea. We found significant differences in the abundance and species diversity of fruiting plants in five types of rainforest habitat based on the level of human disturbance. Logging appears to have had negative impacts on the species richness and abundance of fruiting plants.
Intensive logging operations have caused severe damage to forests particularly tree composition, which could lead to changes in food availability for frugivores. Studies in other tropical regions similarly reported that the density of bird-consumed fruiting plants was reduced in selectively logged forest (Heydon & Bulloh, 1997) and in moderate human-modified habitats (Lefevre et al., 2012). Facing the alteration of food availability in logged forest, many frugivorous mammals and birds are able to partially shift their diets towards folivory or insectivory or adapt their foraging behavior (Jansen & Zuidema, 2001). However, obligate frugivores such as fruit bats and cassowaries have been reported to become scarcer in logged forest (Johns, 1997; Pangau-Adam et al., 2015). Logging activities may affect the diversity of food resources, when certain species of fruiting plants are selectively removed. In our study area, forest trees producing large fleshy fruits such as Cryptocarya, Terminalia and Canarium are amongst the most sought as target species for logging, at local, national and international level. Numerous Papuan forest trees that produce large fruits also have high-quality timber, and are therefore the top choices for extraction (Forestry Services of Papua Province, 2001). In addition, logging operations can lead to a critical decline or even elimination of reproductive individual tree species (Johns, 1997; Meijaard et al., 2005), especially of the rare species and of those that start fruiting above the minimum diameter for logging (Long Ngo & Holscher, 2014; Plumptre, 1995).

An increasing level of disturbance was associated with a decline in canopy cover and tree height. Logged habitat had a high proportion of gap area after exploitation, causing a decreased canopy cover and lower average tree height. Microclimatic conditions, especially light intensity, may change in gaps and forest edges, and lead to increased temperatures (Hardwick et al., 2015). As a result, a high level of soil desiccation may occur, causing lower survival and reproduction of shade-tolerant trees (Costa & Magnusson, 2003). Several fruiting plants are still found in logged forest, including palms, Microcos, Ficus and Syzygium.

Anthropogenic disturbance and the opening of forest canopy were also associated with changes to plant community structure in this rainforest ecosystem. Twenty three species of fruiting plants occurring in undisturbed and hunted primary forests were not found in the three disturbed habitats (Supplementary materials, Table 2). This may indicate the strong influence of forest disturbance on certain fruiting plants, especially canopy trees such as Canarium spp., Aleurites sp., Cryptocarya spp., Instia bijuga and Millettia pinnata. Conversely, several fruiting plants may benefit from anthropogenic forest disturbance as shown through the presence of four fruiting plants that were only recorded in agriculture.

Hunted primary forest had low levels of disturbance, and hence the vegetation structure and fruiting tree abundance were similar to those in undisturbed primary forest. Most of the secondary forest is still recovering from past disturbances, but this habitat had a high number of fruiting plants that can provide food sources for frugivores. The abundance of fruiting plants appeared high in the secondary forest, because certain trees may get benefit from changes in microclimate, especially the improved light conditions through human activities. This has also been recorded in the moderately disturbed habitats in Neotropical forests (Gomes et al., 2008; Lefevre et al., 2012). However, the species composition in disturbed forest is different from that of primary forest, being characterized by more light-demanding pioneer plants, and may likely result in different spatio-temporal fruit availability and even the complete loss of certain fruiting plant species.

Although agricultural areas have a low canopy cover and thick understory vegetation, forest tree species still remain. Four sites of this habitat were adjacent to secondary and hunted primary forest and had fruiting plants of the genera Terminalia, Garcinia, Cerbera, and Actinorhysis, which produce fleshy fruits. These sites could attract frugivorous animals such as cassowaries, especially sub-adult birds, for foraging (Pangau-Adam et al., 2015). As also occurs in Papua New Guinea (Marsden & Pilgrim 2003), traditional agricultures generate a complex land use mosaic that includes secondary forest and/or abandoned logged forest with cultivated plant species and forest vegetation. This habitat type can play an important role in the livelihood of local communities, and can be useful feeding habitat for certain frugivores if it contains forest fruiting plants.

In New Guinea, the family Arecaceae (palms) is among the plant families that are most important for specialist frugivores like cassowaries, and provides a variety of fruits in the lowland forest (Pangau-Adam & Muehlenberg, 2014). Palms were common in each habitat that we studied, and three species producing bird-favored fruits were found in each habitat. Moreover, figs (Ficus spp.) are widespread in this region and found in each habitat studied. Palms and figs may play critical roles as keystone food resources for the frugivorous fauna during seasonally lean periods because they have continual phenology patterns at the population level (Kinnaird & O’Brien, 2005; Wright, 2005). Figs meet important nutritional needs, especially calcium in otherwise mineral-poor diets (O’Brien et al., 1998) and many palm fruits have high levels of protein and fat (Snow, 1981).

A number of frugivorous animals have also been observed directly in the study sites (Table 2 Supplement material), among which some are also
considered being seed predators, e.g. parrots and ground pigeons. Frugivorous species feed upon a wide array of fruiting plants, and bird families in New Guinea are significantly associated with different types of fruits and fruit sizes (Brown & Hopkins, 2002; Pratt & Stiles, 1985). We observed some of the fruiting plant species to have been attracting seed predators, e.g. Victoria crowned pigeons visiting feeding grounds of cassowary, also consumed fallen fruits. Importantly, seed predation is a plant-animal interaction regulating plant coexistence and community assembly processes in forest ecosystems (Larios et al., 2017).

**Implications for Conservation**

Most of the fruiting plants (89%) detected in our study area produce large-sized fruit (as defined by Westcott et al., 2005) and consequently have large seeds. Mack (1993) documented that many trees in New Guinean rainforest have relatively larger fruits than those in forests elsewhere. This may indicate the significance of large-gaped frugivores like cassowary birds (Casuariidae) and hornbills in the seed dispersal process. Forest plants with large fruits and seeds have been found being a major part of the diet of cassowaries in New Guinea (Pangau-Adam & Brodie, 2015; Wright, 2005). Also imperial pigeons and fruit-doves (Ducula and Ptilinopus) consume large fruits >10 mm in diameter (Terborgh & Diamond, 1970), thus they play important roles as dispersal agents in Papuan forest. Because Papua lacks large-bodied frugivorous mammals that would be important for the dissemination of large seeds (Mack & Wright, 2005), these frugivorous birds are considered critical seed dispersers in the Papua region. Unfortunately, large frugivores have been extirpated from much of their natural range through hunting and habitat destruction (Johnson et al., 2004; Wright, 2005). Little is known about how logging affects frugivorous animals in Papua, the only existing studies have reported that northern cassowary (Casuarius unappendiculatus) and the Victoria crowned pigeon (Goura victoria) are found at lower abundance in logged forests (Keiluhu et al., 2019; Pangau-Adam et al., 2015). The differences in cassowary density between habitats was attributed to the variation of fruiting plants and vegetation structure (Pangau-Adam et al., 2015). Further study is needed to assess the impact of logging on population abundance of other frugivorous birds in the Papuan lowland forest, which is threatened by rapid development and increased deforestation. Disappearance of these frugivores may affect the abundance and extinction probability of large-fruited plants in Papua. Therefore, it is imperative to conserve the mutualistic interaction between fruiting forest plants and cassowaries for the persistence and regeneration of Papuan rainforests.

Illegal logging poses serious problems for the protection of Papuan rainforest, and can only be addressed by effective law enforcement and community-based forest management. Former logging areas could be managed and restored with the involvement of local communities as a tool to address illegal logging (Pohnan et al., 2015). An existing collaboration between local communities of Nimbokrang, the Universitas Cenderawasih Jayapura, University of Göttingen, and a conservation NGO, led to a program called ‘Integrating forest management with biodiversity education’. It supports local communities in managing and utilizing their traditional forest (hutan adat) as eco- and wildlife tourism sites. Illegal loggers and wildlife hunters have been recruited to become bird watching guides and workers of the Isyo Hill eco-tourism center. Another restoration effort is planned with stakeholders in this region: it uses the approach suggested by Harrison and Swinfield (2015) to couple restoration goals with income generation and seems to be suitable for Nimbokrang and Nimboran areas. Forest restoration and the involvement of local people are important components to reduce logging activities in Papuan rainforest.

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**Supplemental Material**

Supplementary material for this article is available online.
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