

Research Article

Cite this article: Rueangket A, Duengkae P, Thinkampheang S, Enright NJ, and Marod D (2021) Fruit traits of tree species in lower montane rainforest at Doi Suthep–Pui, northern Thailand. *Journal of Tropical Ecology* **37**, 240–251. <https://doi.org/10.1017/S0266467421000377>

Received: 10 July 2020
Revised: 23 June 2021
Accepted: 9 August 2021
First published online: 9 September 2021

Keywords:

frugivory; fruit colour; fruit size; fruit types; resource availability

Author for correspondence:

Dokrak Marod, Email: dokrak.m@ku.ac.th

#These authors contributed equally to this work.

Apisada Rueangket^{1,†}, Prateep Duengkae¹, Sathid Thinkampheang²,
Neal J. Enright³ and Dokrak Marod^{1,4,†}

¹Department of Forest Biology, Faculty of Forestry, Kasetsart University, Bangkok 10900, Thailand; ²Cooperation Centre of Thai Forest Ecological Research Network, Kasetsart University, Bangkok 10900, Thailand; ³Environment and Conservation Sciences, School of Veterinary and Life Sciences, Murdoch University, Perth, WA 6150, Australia and ⁴Center of Advanced Studies in Tropical Natural Resources, NRU-KU, Kasetsart University, Bangkok 10900, Thailand

Abstract

Fruits are a major food resource for wildlives and have evolved different traits which attract specific frugivores and facilitate seed dispersal. This study examines the quantity of the frequency of fruit tree species, distribution amongst fruit traits and estimates the potential availability of the fruit resource for frugivores in a 16-ha permanent forest plot at Doi Suthep–Pui, Thailand. The similarity amongst traits for fleshy fruited species was explored using Principal Component Analysis (PCA). Fleshy fruited species comprised 122 of 208 tree species >2 cm diameter at breast height (DBH) recorded in the permanent plot. Amongst fleshy fruited species, small fruits (length <20 mm) were most common (63.16% of species) while large fruits were rare (4.1%). Black was the most common fruit colour (43.4%). Principal Component Analysis of fruit traits explained 57% of total variance on the first three axes, and allowed identification of three species groups. *Litsea martabanica* and *Persea gamblei* are the greatest density and represented the major PCA group; black, small-sized and thin husk indehiscent fruits. These fruiting trees scattered throughout the permanent plot and were of good regeneration status. Indicating fleshy fruit can be a food resource for frugivores especially small-sized fruit. Furthermore, large-fruited species such as *Madhuca floribunda* is low density but important to preserve for food resource of large frugivores. This finding is very important not only for forest protection policy but also for wildlife conservation as food resources.

Introduction

Fruits are reproductive organs of plants that contain and protect seeds while they are developing for germination (Nathan & Chee 1987). Another function of fruits is to attract frugivores to help seed dispersal (Nathan & Chee 1987), moving seeds away from parent trees to avoid competition and pathogens and increase the chance of seedling establishment (Corlett 2014). There are many factors to help seed dispersion such as gravity, water, wind or animal but animals are the main factor. Plant species have evolved different fruit traits to attract seed dispersion factors, especially specific frugivores (Van der Pijl 1982), with a range of fruit traits reported to influence fruit choice of frugivores including size (Chen *et al.* 2004; Flörchinger and Braun 2010; Galetti *et al.* 2011; Kitamura *et al.* 2002), type of fruits (Chen *et al.* 2004; Stiles 1989), colour (Chen *et al.* 2004; Galetti *et al.* 2011; Gautier-Hion *et al.* 1985; Kitamura *et al.* 2002; Wheelwright & Janson 1985), physical protection of fruits (Chen *et al.* 2004; Gautier-Hion *et al.* 1985), nutrients (Flörchinger & Braun 2010; Kitamura *et al.* 2002) and phenology (Chen *et al.* 2004), as well as seed traits such as seed size (Chen *et al.* 2004; Galetti *et al.* 2011; Kitamura *et al.* 2002), seed protection (Chen *et al.* 2004; Gautier-Hion *et al.* 1985) and seed number (Chen *et al.* 2004; Gautier-Hion *et al.* 1985; Kitamura *et al.* 2002). Fruit size is an important trait that affects seed dispersal because fruit size relates to body size of frugivores. Large frugivores disperse large fruits and small frugivores disperse small fruits (Galetti *et al.* 2013; Guimarães *et al.* 2008).

Tropical forests are renowned for their high diversity of both flora and fauna (Brown 2014), with most plant species producing fruits which are important food resources for frugivores (Kimura 2003). Tropical forests are under threat from land clearance, degradation and conversion to agriculture (Elliott & Kuaruksa 2008), with forest loss and fragmentation leading to a reduction in the frugivore food supply and potential population decrease or local extinction of both fruit-dependent vertebrate species and the plants whose fruits they disperse (Dirzo *et al.* 2014; Sekercioglu *et al.* 2004; Tylisanakis 2013). Furthermore, poaching is a cause of frugivores decline or extinction result of seed disperser loss that leads to plant population decline and extinction (Loiselle *et al.* 2002). Tropical montane forests are particularly vulnerable because their recovery is typically slower than that of lowland forests due to the less favourable

climate for plant growth (Crausbay & Martin 2016). They are therefore likely to be especially vulnerable to the adverse impacts of forest loss, fragmentation and degradation. A sound understanding of the frugivore–plant relationships in tropical montane forests is thus essential to their ongoing conservation and management.

In this study, we examine the fruit traits for tree species in a 16-ha permanent forest plot established in 2010 in the Huai Kog Ma watershed area, Doi Suthep–Pui National Park, Chiang Mai Province, northern Thailand. The objectives of this research were to quantify the frequency of fruit occurrence in the lower montane forest and distribution of fruit traits amongst species; and to estimate the potential availability of the fruit resource available to frugivores and how it varies amongst species characterized by different fruit trait sets.

Study site

This study was conducted at the 16-ha permanent forest measurement plot within the Huai Kog Ma watershed area (18° 54'N longitude and 98° 54'E latitude) located in Doi Suthep–Pui National Park, Chiang Mai Province, northern Thailand (Figure 1). The watershed has an elevation range from 1,250 to 1,540 m above mean sea level (Vongkuna 2005). The area has a strongly seasonal climate with a wet season from May to October (mean wet season rainfall 1,219 mm y^{-1} over the 10-year period 2009–2018; Doi Suthep–Pui Climate Station 327020) and dry season from November to April (mean dry season rainfall 119 mm y^{-1}). The mean daily maximum temperature in the wet season during the same period was 28°C and 21.8°C in the dry season.

The permanent plot was conducted in the lower montane forest at Mae Sa–Kog Ma biosphere reserve. The permanent plot consists of large trees with a canopy up to 30 m high. The indicator plant species in the lower montane forest are plants in Fagaceae with some mixed species in gymnosperm (Marod & Kutintara 2009). The dominant families in the permanent plot are Lauraceae, Euphobiaceae and Fagaceae (Marod *et al.* 2015). While animals in the permanent plot were found, many animals were in four groups such as mammals, birds, amphibians and reptiles. The examples of animals are Leopard cat, Hog badger, Common palm civet, Red-cheeked squirrel, Silver pheasant, Ashy bulbul, Puff-throated bulbul, Himalayan newt, Twin-spotted tree frog, Common mock viper and Pope's pit viper, etc. (Duengkhae & Marod 2016). However, the permanent plot is located close to villages. So sometimes, we found the villagers came to collect forest products such as mushrooms and some tourists.

Methods

The 16-ha permanent plot (400 m × 400 m) was set up in 2010 and is divided into marked subplots of 100 m², totalling 1,600 subplots. All trees with diameter at breast height (DBH) ≥ 2 cm were tagged, measured and identified (Marod *et al.* 2015). Data on tree and fruit parameters for all tree species identified within the permanent plot were collected from both primary and secondary sources. Primary source information was obtained by direct observation in the permanent plot (found these species provided fruits) and subsequent measurement of data for collected fruits of 10 species (5–30 replicate fruits per species depending on availability): *Choerospondias axillaris*, *Madhuca floribunda*, *Schefflera heptaphylla*, *Baccaurea ramiflora*, *Apodytes dimidiata*, *Ficus curtipes*, *Ficus hirta*, *Ficus semicordata*, *Prunus arborea* and *Acronychia pedunculata*.

Secondary sources were mainly online databases and publications including the Concise Encyclopedia of Plants in Thailand database (Forest Botany Division 2016), The Botanical Garden Organization databases (The Botanical Garden Organization 2011), the Useful Tropical Plants database (Fern 2014) and a field guide to forest trees of northern Thailand (Gardner *et al.* 2007). We collected data on 10 fruit traits for the focused tree species and categorized each trait into the same scale for easy to analyse as the following.

The definition of trait categories for fruits was as follows:

Life form: vine (stem DBH >2 cm), large shrub (2 cm DBH to 7 m height), small tree (height 7–15 m), middle-sized tree (height 15–30 m), tall tree (height >30 m) – following Kitamura *et al.* (2002).

Dispersal mode: barochory (seeds dispersed by gravity), ballistichory (dispersed by launching), anemochory (wind), endozoochory (eaten and pass through animal gut), hoarding (buried or otherwise cached by animals) – following Cornelissen *et al.* (2003).

Fruit type: fleshy – cone, drupe, berry, syconia; non-fleshy – nut, aggregate fruit, capsule – following Stiles (1989).

Fruit size: measured as length of longest axis; small (<20 mm), medium (20–50 mm), large (>50 mm) – following Chen *et al.* (2004).

Fruit colour: green, yellow, brown, orange, red, blue, black (includes dark purple) – following Wheelwright and Janson (1985).

Fruit protection: measured as presence and thickness of an outer barrier which reduces access to the flesh and seeds; dehiscent (there is no barrier), indehiscent with thin husk (a thin skin that can be cut with a fingernail), indehiscent with thick husk (a thickened wall) – following Gautier-Hion *et al.* (1985).

Fruiting season: dry season (November–April), aseasonal (throughout the year or more than one time per year), wet season (May–October) adapted from Chen *et al.* (2004).

Number of seeds per fruit: few (1–3 seeds), some (4–10 seeds), many (>10 seeds) – following Chen *et al.* (2004).

Seed size: seed length; small (<2 mm), medium (2–10 mm), large (>10 mm) – following Chen *et al.* (2004).

Seed protection: no protection, thin seed coat (the seed coat can be opened with a fingernail), thick seed coat (the seed coat is lignified or there is a true stone) – following Gautier-Hion *et al.* (1985).

The trait data were sorted by the number and proportion of species in each category. Because fruit resource to selection by frugivores is also determined by body and gape size of frugivores and fruit size, (Chen *et al.* 2004; Corlett 1998), we first examine the relationship between fruit size and all other fruit and seed traits by χ^2 because the data were measured in categorical scale. We then use Principal Component Analysis (PCA) to examine further the similarities amongst fruit traits using function `prcomp` in the R software stats package (R Core Team 2019). Fruit traits were assigned ordinal values increasing from 0 (starting from the first category until the last category) for each trait category (order as listed above under trait category descriptions). Then hierarchical cluster were analysed for divided groups of fruiting species. Furthermore, the distribution maps of fruiting trees cluster from PCA analysis were created.

The food resource available to frugivores was estimated based on the density, basal area and stem size–class distributions for each fleshy fruited species in the 16-ha permanent plot with

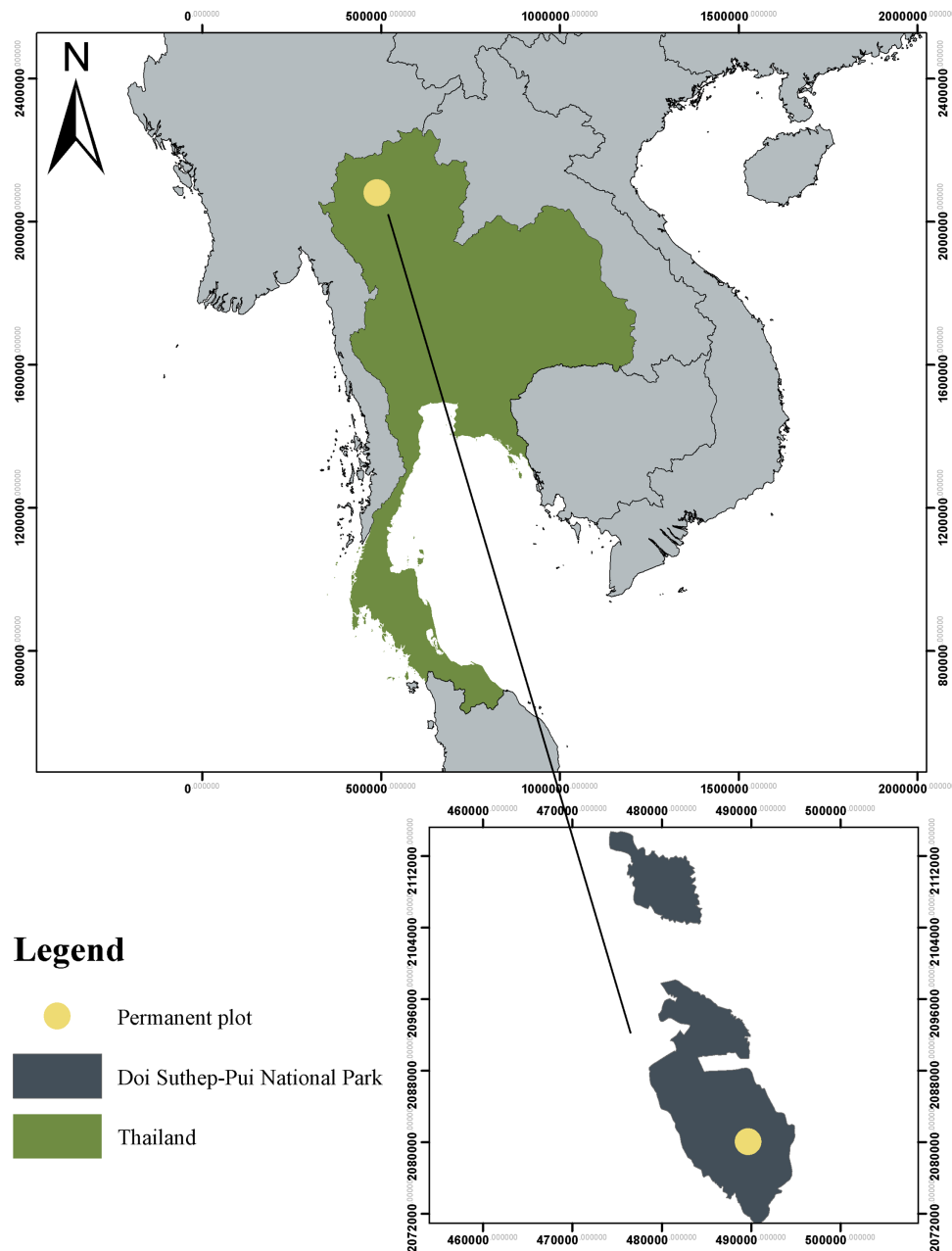


Figure 1. Study area location (Huai Kog Ma watershed) in lower montane forest, Doi Suthep–Pui National Park, Thailand.

DBH ≥ 2 cm. Trees with DBH < 5 cm were considered to be juveniles, and while included for size–distribution analysis, were excluded from density and basal area estimates since they are unlikely to contribute to fruit production. Given that annual fruit/seed crop size generally increases with tree size (Harper 1977), tree species were ranked by density (ha^{-1}) and basal area ($\text{m}^2 \text{ha}^{-1}$) as a measure of fruit resource availability for frugivores. The DBH size distributions of fleshy fruited trees were described using 26 classes (DBH 2–5 cm, and then every 5 cm up to DBH > 125). Size distributions were used to assign species to regeneration type categories of either light-demanding (fewer individuals in the smallest size classes) or shade-tolerant (inverse J distribution of size–class abundances) (Gairola *et al.*, 2014; Melese & Ayele, 2017; Swamy *et al.*, 2000). If the generation status is reverse-J shape, mean mature trees of plant population are replaced by new

trees of the next generation (Larson & Funk, 2016), indicating good regeneration. When fruiting species has good regeneration indicating they have the potential to provide fruits for frugivores in the future. All statistical analyses were conducted using R software version 3.5.3 (R Core Team 2019).

Results

General flora

The 16-ha permanent plot contained a total of 29,163 individuals 208 woody species in 139 genera and 59 families. Life forms included 81 species of middle-sized trees (38.9%) or 13,978 individuals (47.9%), 77 small trees (37.0%) or 10,130 individuals (34.7%), 28 shrubs (13.5%) or 3,479 individuals (11.9%), 21 tall

trees (10.1%) or 1,567 individuals (5.4%) and 1 vine (0.5%) or 9 individuals (0%). Dispersal mode across all species was dominated by endozoochory (157 species; 75.5% or 17,268 individuals, 59.2%), followed by ballistichory (26 species; 12.5% or 3,210 individuals, 11.0%), hoarding (16 species; 7.7% or 7,373 individuals, 25.3%) and anemochory (9 species; 4.3% or 1,312 individuals, 4.5%). Of the total of 173 species with animal consumed fruits (83.2%) (24,641 individuals), 122 species were fleshy fruited (70.5%) (12,562 individuals) and 51 were non-fleshy fruited (29.5%) (12,081 individuals). The density of all tree species ≥ 2 cm DBH in the permanent plot was 859 ha^{-1} , and of fleshy fruited species was 358 ha^{-1} . The mean basal area of trees ≥ 2 cm DBH across all species was $34.5 \text{ m}^2 \text{ ha}^{-1}$ and for fleshy fruited species was $12.9 \text{ m}^2 \text{ ha}^{-1}$.

Fleshy fruits

Amongst the fleshy fruited species 62 (50.8%) or 7,516 individuals (59.8%) produced berries, followed by 52 (42.6%) of 4,921 individuals (39.2%) with drupes, 6 (4.9%) or 87 individuals (0.7%) with syconia and 2 (1.6%) or 38 individuals (0.3%) with cones. The highest proportion of fleshy fruited species were small trees (42.6% of species or 44.1% of individuals), followed by middle-sized trees (30.3% of species or 34.0% of individuals), shrubs (18.9% of species or 13.9% of individuals) and tall trees (8.2% of species or 8.0% of individuals). Most fleshy fruited species produced black fruits (43.4% of species or 57.1% of individuals). The next most common colours were red and yellow (19.7% of species or 7.5% of individuals and 14.8% of species or 11.0% of individuals, respectively). Brown, orange, green and blue fruits were relatively rare (7.4%, 6.6%, 4.1% and 4.1% of species, respectively, or 5.0%, 9.5%, 6.9% and 3.1%, respectively). The majority of fleshy fruits (63.1% of fleshy fruited species or 74.1% of individuals) were small (length < 20 mm), followed by medium-sized (40 species; 32.8% of species, 25.3% of individuals) and large (5 species; 4.1% of species, 0.5% of individuals) large fruits.

Fruit size and life form

The distribution of fruit sizes did not differ significantly amongst life forms ($\chi^2 = 11.304$, $df = 6$, $P = 0.08$). Most species bearing large fruits (80%) were small trees. Half of the small-sized trees (50%) produced medium-sized fruits. Most small fruits were associated with small trees (36.4%), middle-sized trees (29.9%) and shrubs (26%) (Figure 2a).

Fruit size and fruit season

The distribution of fruit size differed significantly by fruiting season ($\chi^2 = 7.260$, $df = 4$, $P = 0.12$). Most plant species produced fruit in the wet season. Most middle-sized fruits were produced in the wet season (62.5%) or dry season (25%). Most small fruits were produced in the wet season (58.4%) or dry season (39%). While most large-fruited species produced fruits in the wet season (60%) or equally in dry season and throughout the year (20%) (Figure 2b).

Fruit size and fruit type

Fruit type differed significantly by fruit size ($\chi^2 = 16.269$, $df = 6$, $P < 0.05$). Most plants bearing small fruits were characterized by berries and drupes (54.5% and 42.9%, respectively), while medium fruits were predominantly berries, drupes and syconias (47.5%,

40% and 12.5%, respectively). Large fruits were either berries (80%) or syconias (20%) (Figure 2c).

Fruit size and colour

Fruit colour differed significantly by fruit size ($\chi^2 = 28.267$, $df = 12$, $P < 0.05$). Black (51.9%) was the dominant colour for small and medium-sized fruits followed by red (20%). Yellow (40%) green (20%) and orange (20%) occurred in large fruits, while brown and blue colours were rare across all fruit sizes (Figure 2d).

Fruit size and fruit protection

Different sized fruits differed significantly in fruit protection ($\chi^2 = 32.424$, $df = 4$, $P < 0.0001$). Most small fruits (85.7%) were indehiscent with a thin husk. Both types of indehiscent fruits – with thin husk (50%) and thick husk (50%) – occurred in medium-sized fruits. Most large fruits (80%) were indehiscent with a thick husk. Dehiscent fruits occurred only in small fruits (Figure 2e).

Fruit size and seed characters

All species produced either medium seeds or small seeds regardless of fruit type. Seed size differed significantly from fruit size ($\chi^2 = 8.693$, $df = 2$, $P < 0.05$). Most small fruits (87%) had small seeds (length < 2 mm) while most large fruits had small seeds (60%) or medium seeds (40%) (Figure 2f). Most species with both small-sized fruits (80.5%) and medium-sized fruits (67.5%) bear fruits with few (1–3 seeds per fruit) seeds per fruit. Most large fruits bear fruits with some (4–10 seeds per fruit) (60%) or many (> 10 seeds per fruit) seeds per fruit (40%) (Figure 2h). The distribution of seed protection types also differed significantly with fruit size ($\chi^2 = 6.649$, $df = 2$, $P < 0.05$). Large (80%), medium (52.5%) and small (75.3%) fruits had mostly thick seed coats (Figure 2g).

Similarity amongst fruit traits

The first three factors of the PCA conducted on the fruit traits by species matrix accounted for 56.7% of the total variation. The first factor is most strongly related to fruit protection, number of seeds per fruit, fruit size and fruit type, all having large negative loadings (Table 1). This axis separates species with fruits containing many seeds and thick husk indehiscent fruits from other species (Figure 3). The second factor is most strongly related to seed size, life form and fruit type. Seed size and life form influenced it negatively, while traits related to fruit type have positive loadings. This axis separates species with drupe fruit type and/or large seeds, from the others. The third factor is heavily influenced by fruit season and seed protection. Fruit season had a strong positive loading, while traits related to seed protection has a strong negative loading.

The hierarchical cluster divided fleshy fruited species into 3 groups (Figure 4). The first group consists of 27 species such as *M. floribunda*, *Elaeocarpus* spp., *Ficus* spp., *Baccaurea* spp. and *Garcinia* spp. This group is characterized by species with predominantly medium to large-sized berry fruits, with bright coloured, thick husk indehiscent and containing many seeds. Some species in this group provided fruits throughout the year. The second group is defined by species with predominantly small-sized, thin husk, both dull and light coloured fruits, containing few seeds with small seed and provided fruits in dry season. This group includes 35 species such as *Ardisia quinquegona*, *Canthium glabrum*, *Chionanthus ramiflorus*, *Diospyros kerrii* and *S. heptaphylla*. The last group consists of a large number of species with berry, drupe and cone predominantly small-sized, thin husk, black coloured

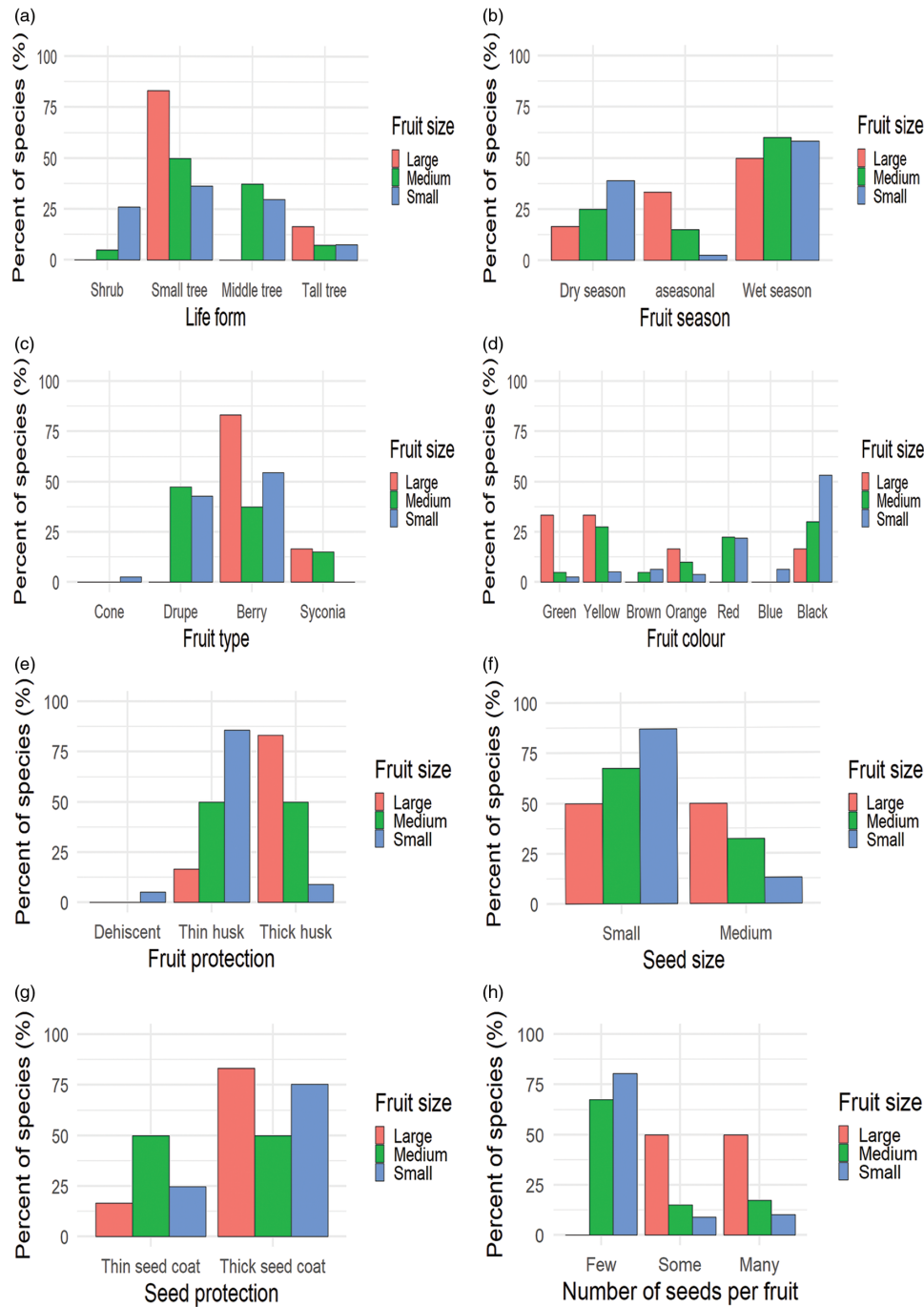


Figure 2. Distribution patterns of different fruit traits against percentage values with summation to 100% for each fruit size class were shown. The abbreviates were different fruit traits; (a) life form, (b) fruit season, (c) fruit type, (d) fruit colour, (e) fruit protection, (f) seed size, (g) seed protection and (h) number of seed per fruits.

fruits, few number of seeds and small seed-sized with thick seed and provided fruit in wet season such as *Alangium kurzii*, *Ilex englishii*, *Casearia grewiifolia*, *Syzygium* spp., *Litsea* spp. and *Cinnamomum iners*. When considering the distribution maps of fruiting trees cluster, it was found that all three groups of fruiting trees were distributed throughout the permanent plot (Figure 5a–c). From the fruiting trees, distribution maps of three groups found the fruiting trees are scattered throughout the permanent plot. In some areas, each group of fruiting trees had different densities.

Food resource for frugivores

The fleshy fruited species with the greatest density is *Litsea mar-tabanica* followed by *Persea gamblei* and *Saurauia roxburghii*, respectively. The fleshy fruited species with the greatest basal area is *Litsea grandis* followed by *Syzygium toddlioides* and *C. axillaris*, respectively. Group 3 had the greatest total density and basal area (440.9 trees ha⁻¹, 9.44 m²ha⁻¹), followed by group 2 (216.4 trees ha⁻¹, 2.47 m²ha⁻¹) and group 1 (127.7 trees ha⁻¹, 1.26 m²ha⁻¹), respectively (Table 2). This result indicates that

Table 1. PCA factor loadings, eigenvalues and % variance explained for the first three axes of the fleshy fruited tree species by fruit traits data matrix

Fruit traits	PC1	PC2	PC3
Life form	0.03	-0.45	0.07
Fruit type	-0.43	0.43	0.20
Fruit colour	0.38	0.25	0.17
Fruit protection	-0.49	-0.14	-0.14
Fruit size	-0.44	-0.36	0.09
Number of seeds per fruit	-0.46	0.24	-0.12
Seed size	-0.03	-0.52	0.01
Seed protection	0.14	-0.15	-0.62
Fruit season	0.04	-0.21	0.71
Eigenvalue	2.36	1.56	1.16
Cumulative % variance	26.28	43.63	56.54

the majority of individuals (>90%) and basal area (~90%) of fleshy fruited species within the 16-ha forest plot have black, small-sized and thin husk indehiscent fruits. The other groups with medium-large-sized, thick husk indehiscent fruits containing medium-sized seeds and many seeds are represented by few, and primarily small, trees.

The overall DBH size-class distributions for fleshy fruited species for each of the three PCA groups were strongly negative exponential with highest frequencies in the smallest diameter classes (Figure 6a–f). Species in group 1 had few individuals larger than 30 cm DBH, while the summed distributions for groups 2 and 3 showed a long tail of larger trees (up to 125 cm DBH). These same patterns were shown also for the species contributing the highest basal area in PCA group 1; *D. glandulosa* mostly comprising small trees with negative exponential pattern (Figure 7a–f). For groups 2 and 3, the highest basal area species, *L. grandis* and *C. axillaris* showed lower frequencies in the smallest size class than in the next larger class.

Discussion

Of the total 122 species of fleshy fruits, small trees (42.6%) had the highest proportion followed by middle-sized trees, shrub and tall trees, respectively. A Tropical seasonal forest in Thailand, Kitamura *et al.* (2002), found shrub is the highest proportion followed by middle-sized trees, liana, small trees, tall trees, herbs and epiphytes. Amongst fleshy fruited species, there were strong patterns in the fruit traits displayed amongst tree species: The majority of species with fleshy fruits were characterized by small fruit size, black in colour, thin protective coats, medium seed size and few seeds per fruit, consistent with the findings of Chen *et al.* (2004), Galetti *et al.* (2011), Gautier-Hion *et al.* (1985), Herrera (1987), Kitamura *et al.* (2002), Peña *et al.* (2020).

Fleshy fruits are the primary forest food resource for frugivorous birds and mammals (Jordano 1992). Each frugivore species likely prefers fruits that have different traits, with the extent of fruit type specialization influencing frugivore species abundances and distributions. Fruit size is an important trait in fruit selection by frugivores, (Peña *et al.* 2020 & Valenta *et al.* 2020), with selected fruit size related to mouth size (Valido *et al.* 2011) – i.e. large fruits consumed more often by large frugivores and small fruits by small frugivores (Flörchinger & Braun 2010). Fruit colour also affects the fruit visitation of frugivores. Mammals and birds have different colour visual systems (Corlett 2011), and many authors report that birds prefer red and black fruits while mammals are more likely to choose yellow and green fruits (Galetti *et al.* 2011; Gautier-Hion *et al.* 1985; Kitamura *et al.* 2002). Furthermore, Kitamura *et al.* (2002) note that both large and small soft fruits with many seeds are eaten by a broad array of frugivore species (bird and mammal), while fruits with single large seeds are eaten by fewer frugivore species, and mostly not by small frugivores. So, tree species with fruits having these traits (large fruit size, and yellow or green in colour) may be at higher risk of decline under human impact on forest ecosystems, with large frugivores often preferentially lost from fragmented forest patches. A previous study in the Doi Suthep–Pui large plot (Rueangket *et al.* 2019) reported that *M. floribunda* fruits (large green, thick husk, moderate seeds)

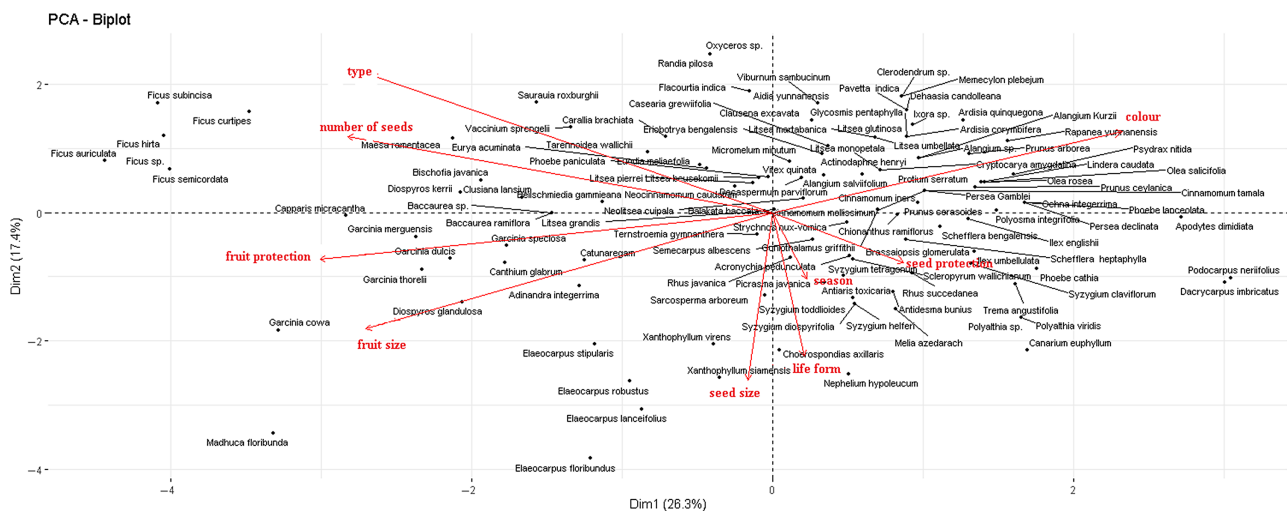


Figure 3. Distribution of fleshy fruited tree species and fruit trait biplot vectors for the first two axes of the species x fruit traits matrix PCA. Points show the position in ordination space of each tree species, and vectors show the direction of maximum correlation and positive increase in fruit trait values. Length of vectors shows their relative importance. The first axis explains 26.3% of total variation, and the second axis 17.4%.

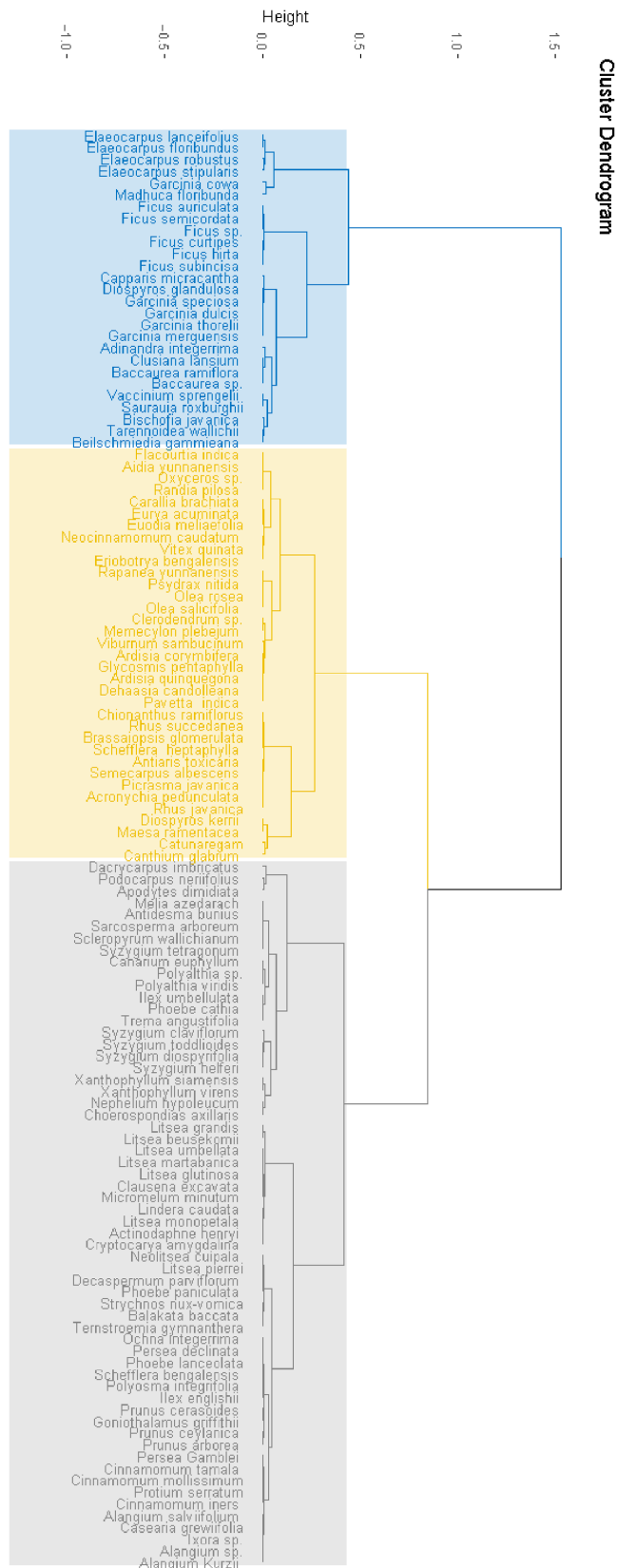


Figure 4. The result of hierarchical cluster analysis can divide fleshy fruited species into three groups.

were consumed by many species of frugivore, particularly rodents, while the small fruits of *Schefflera* sp. were consumed only by bulbuls. In addition, the season of fruit ripening may also strongly influence fruit resource available to frugivores. In our study, and consistent with Chen *et al.* (2004), most species show fruit ripening in the wet season, some in the dry season, while only a very small number show aseasonal fruit production.

In our study area, while non-fleshy fruits comprised only 31.7% of species, they comprised a much higher percentage of overall tree density (45%) and basal area (45%) and represent a significant source of food for some animal species, particularly squirrels and rats (Gautier-Hion *et al.* 1985; Vander Wall 2001). These fruit types were mainly nuts from species in the genera *Castanopsis*, *Lithocarpus* and *Quercus* (all Fagaceae), and a previous study (Rueangket *et al.* 2019) found nuts of *Castanopsis acuminatissima* were consumed by only rodents. Rodentia is well known as seed predators but also contribute to the dispersal of seeds through their scatter hoarding and occasional forgotten seed caches, so that some seeds escape consumption and can germinate and establish (Corlett 2017; Suzuki *et al.* 2007; Vander Wall 2010). These animal groups have strong gnawing incisors so they can consume nuts and other thick seed coat fruits which have a hard shell (Corlett 2017).

Although not explicitly explored here, phylogenetic relatedness as a driver of fruit trait similarities amongst species was apparent. Most species in our PCA group 1 represented well-protected, medium to large fruits, small to medium seed size. Group 2 represented the species with predominantly small-sized, thin husk, both dull and light coloured fruits, containing few seeds with small seed and provided fruits in dry season. And group 3 represent small-sized, thin husk, black coloured fruits, few number of seeds and small seed-sized with thick seed and provided fruit in wet season. Chen *et al.* (2004) noted phylogenetic relatedness particularly in relation to number of seeds per fruit, and fruit and seed protection, the first two of these are also important in our study. Furthermore, Chen *et al.* (2004) found evidence of low fruit size variance in the same genus, which he considered may reflect a selective response to different frugivore species pressures. Fruiting species in group 1 consist of *Ficus* species, we note that *Ficus* is well known as a keystone resource for forest frugivores because almost all types of frugivores (bird, mammal, reptile and fish) consume their fruits across a broad range of fruit sizes (Shanahan *et al.* 2001) and many species of moderate to large fruits (*Garcinia* species, *Elaeocarpus* species and *M. floribunda*), suitable for large frugivores because large frugivores can disperse seeds to long distance to suitable germination and establishment site (Naniwadekar *et al.* 2019), but the species in this group has low density and basal area in this forest, and volume of fruits may be small. This potentially may limit the resource base for some larger sized frugivores, a problem likely to be exacerbated by forest loss and fragmentation, because fragmentation reduces frugivores density and fruit dispersal (Kirika *et al.* 2007). Group 2 and group 3 consist of many small-sized fruits with few seeds but differed in fruit protection and fruit colour and seasonal. These groups have higher densities and basal areas indicated this forest has many small-sized fruits to attract both small and large frugivores like small fruits (Gautier-Hion *et al.* 1985; Wheelwright 1985). However, the frugivores species was attracted to consume fruits must also consider other fruit traits such as fruit colour and fruit season. From distribution map of fruiting, trees that

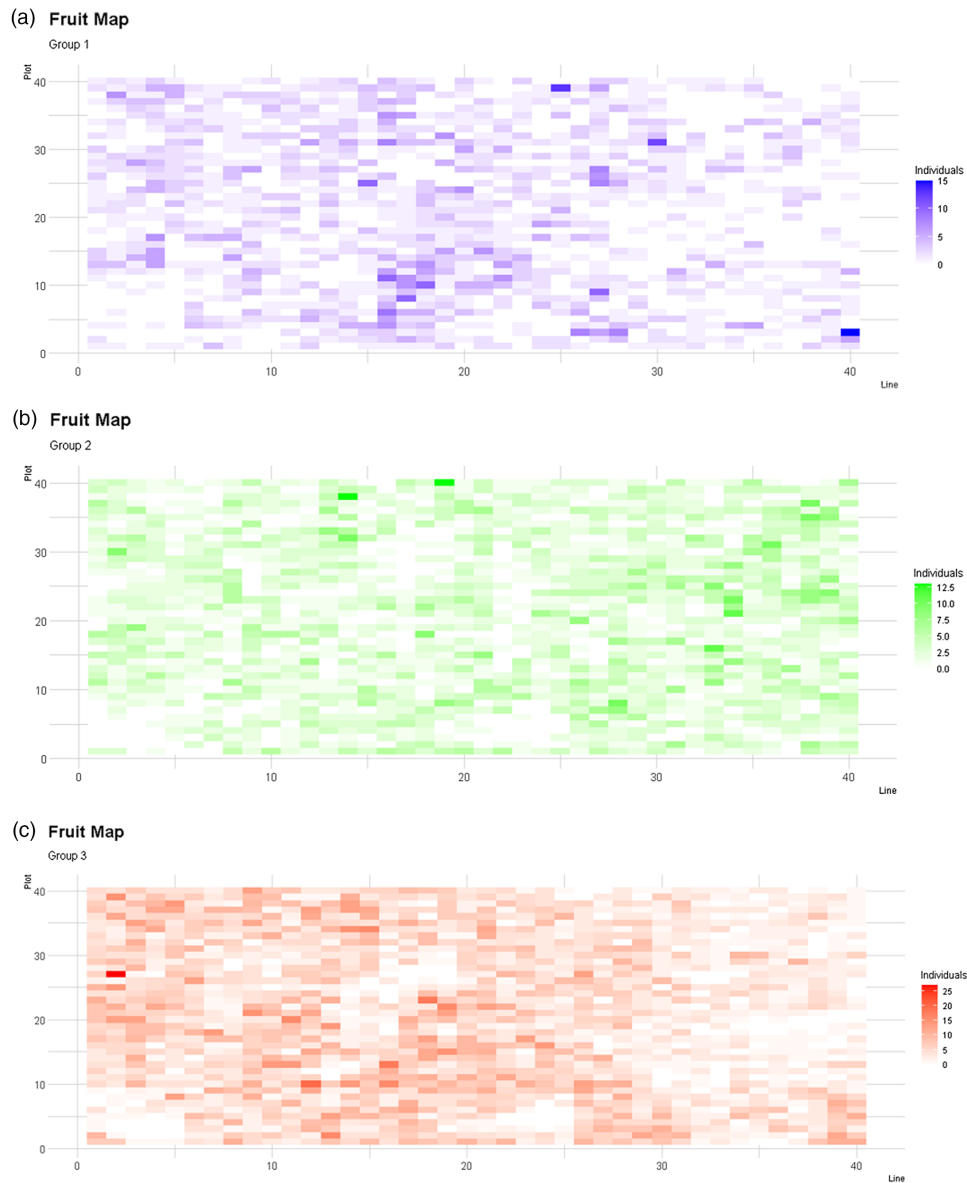


Figure 5. Fleshy fruited trees distribution map by three groups from hierarchical cluster analysis. (a) Group 1; (b) group 2; (c) group 3.

scattered throughout the permanent plot indicated this forest has enough fruits to support frugivores.

Most species size-class distributions showed distributions reflective of stable mature forest dynamics with continuous recruitment supporting population size and structure, as described by Melese and Ayele (2017).

Conclusions

The 16-ha permanent plot has many fleshy fruits that varied fruit traits, predominantly small-sized, black, thin husk, berried

fruits with few, small-sized seeds. The fruited species with these traits occurred in group 3 of hierarchical clustering. The overall fruiting trees in the permanent plot that were higher small-sized class than larger sized class can imply to this area having many fruiting trees for supporting food resource of frugivores in the future because their regeneration status is good. On the other hand, there are lower fruiting tree species, occurred in group 1, suggests a potential bottleneck for resource availability to specialist frugivores which depend on these fruit types and makes them especially vulnerable to decline if forest clearance and fragmentation continues.

Table 2. The density and basal area of fleshy fruited tree species by PCA group in the lower montane tropical rainforest study area at Doi Suthep-Pui, northern Thailand

Species	Density (trees ha ⁻¹)	Species	Basal area (m ² ha ⁻¹)
Group 1			
<i>Saurauia roxburghii</i>	31.0	<i>Elaeocarpus floribundus</i>	0.21
<i>Diospyros glandulosa</i>	11.8	<i>Elaeocarpus stipularis</i>	0.14
<i>Garcinia thorelii</i>	11.1	<i>Tarennoidea wallichii</i>	0.13
<i>Elaeocarpus floribundus</i>	10.6	<i>Saurauia roxburghii</i>	0.12
<i>Baccaurea ramiflora</i>	8.9	<i>Beilschmiedia gammieana</i>	0.12
<i>Tarennoidea wallichii</i>	8.8	<i>Garcinia thorelii</i>	0.10
<i>Vaccinium sprengelii</i>	8.4	<i>Vaccinium sprengelii</i>	0.10
<i>Clusina lansium</i>	7.8	<i>Bischofia javanica</i>	0.08
<i>Elaeocarpus stipularis</i>	4.6	<i>Diospyros glandulosa</i>	0.05
<i>Beilschmiedia gammieana</i>	4.0	<i>Baccaurea ramiflora</i>	0.05
Total	127.7	Total	1.26
Group 2			
<i>Acronychia pedunculata</i>	29.8	<i>Vitex quinata</i>	0.52
<i>Memecylon plebejum</i>	25.4	<i>Semecarpus albescens</i>	0.46
<i>Vitex quinata</i>	24.9	<i>Acronychia pedunculata</i>	0.45
<i>Eriobotrya bengalensis</i>	14.3	<i>Rhus javanica</i>	0.25
<i>Eurya acuminata</i>	13.6	<i>Eurya acuminata</i>	0.13
<i>Rapanea yunnanensis</i>	13.5	<i>Carallia brachiata</i>	0.12
<i>Olea rosea</i>	12.2	<i>Eriobotrya bengalensis</i>	0.09
<i>Semecarpus albescens</i>	11.6	<i>Rapanea yunnanensis</i>	0.09
<i>Maesa ramentacea</i>	10.7	<i>Viburnum sambucinum</i>	0.06
<i>Carallia brachiata</i>	9.1	<i>Schefflera heptaphylla</i>	0.05
Total	216.4	Total	2.47
Group 3			
<i>Litsea martabanica</i>	81.69	<i>Litsea grandis</i>	1.16
<i>Persea Gamblei</i>	59.9	<i>Syzygium toddlioides</i>	1.11
<i>Apodytes dimidiata</i>	29.6	<i>Choerospondias axillaris</i>	0.93
<i>Schefflera bengalensis</i>	28.7	<i>Syzygium tetragonum</i>	0.87
<i>Litsea grandis</i>	18.9	<i>Persea Gamblei</i>	0.65
<i>Sarcosperma arboreum</i>	17.4	<i>Phoebe paniculata</i>	0.58
<i>Cinnamomum iners</i>	16.7	<i>Syzygium claviflorum</i>	0.39
<i>Syzygium toddlioides</i>	16.6	<i>Litsea pierrei</i>	0.35
<i>Canarium euphyllum</i>	15.6	<i>Litsea martabanica</i>	0.34
<i>Syzygium tetragonum</i>	12.1	<i>Sarcosperma arboreum</i>	0.34
Total	440.9	Total	9.44

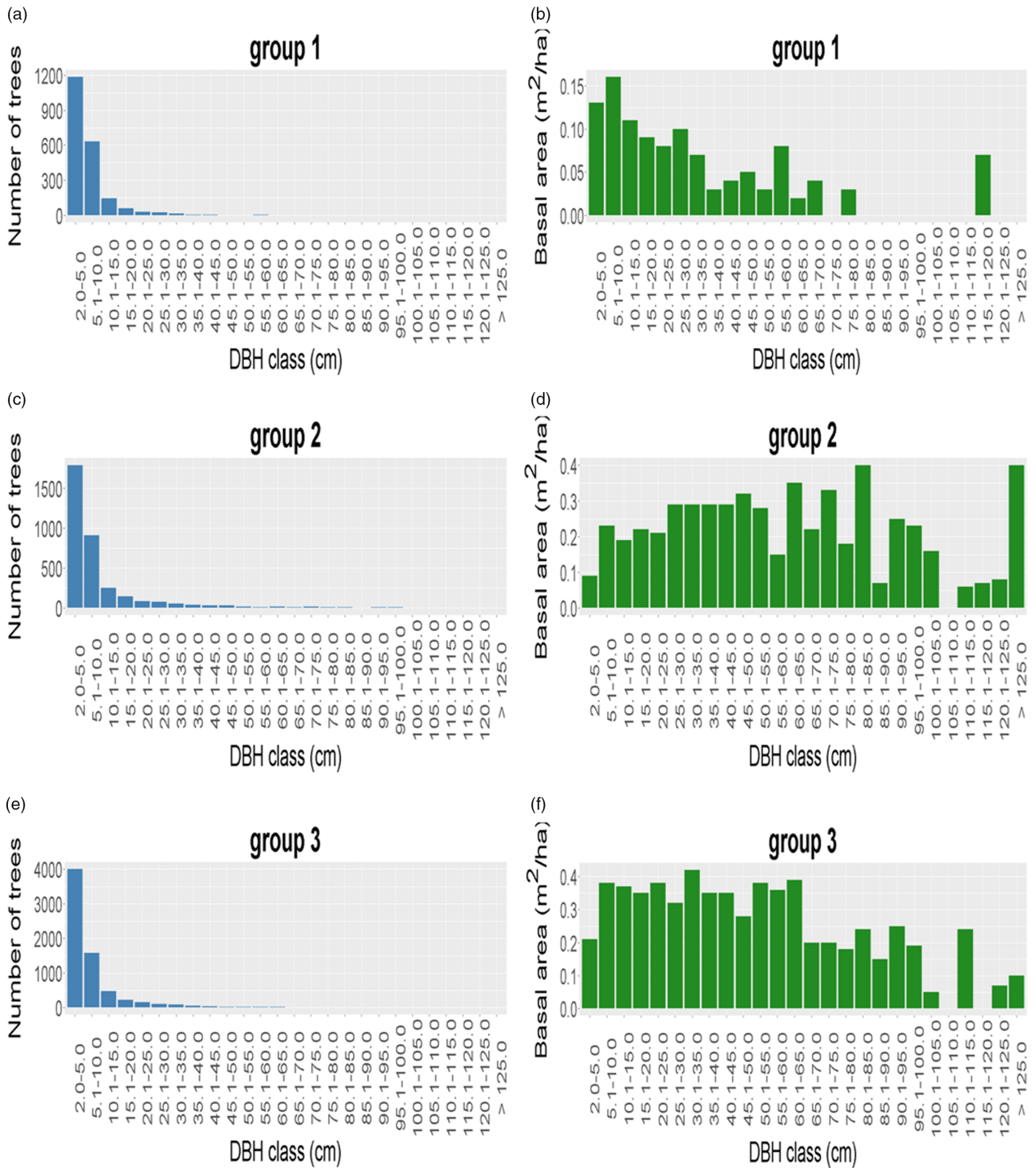


Figure 6. The DBH distribution pattern of fleshy fruit species by PCA grouping and the basal area distribution in each DBH class. (a) The DBH distribution pattern of group 1; (b) The basal area distribution pattern of group 1; (c) The DBH distribution pattern of group 2; (d) The basal area distribution pattern of group 2; (e) The DBH distribution pattern of group 3; and (f) The basal area distribution pattern of group 3.

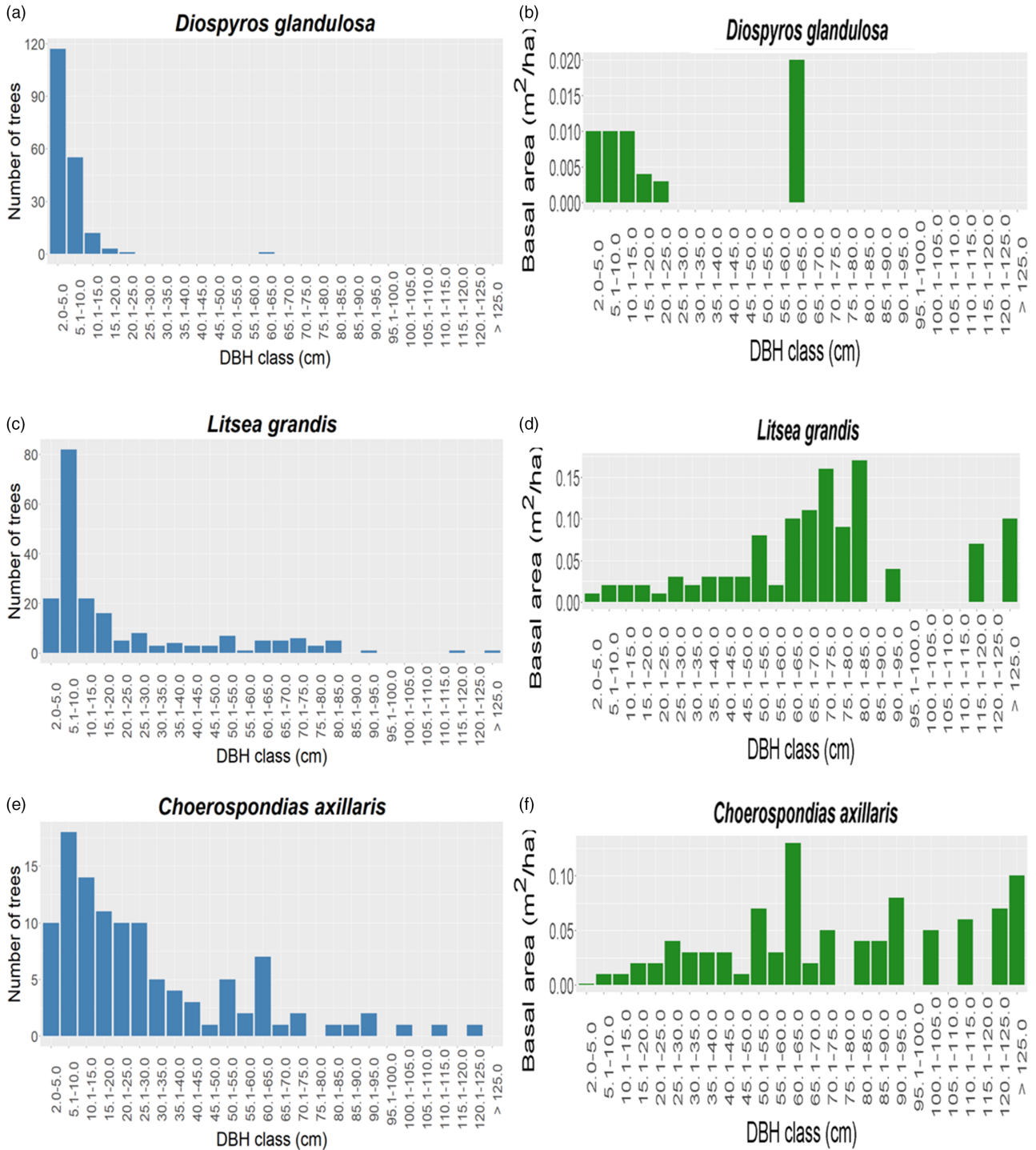


Figure 7. The DBH distribution pattern of fleshy fruit species with the highest basal area in each group and the basal area distribution pattern in each DBH class. (a) The DBH distribution pattern of *Diospyros glandulosa*; (b) The basal area distribution pattern of *D. glandulosa*; (c) The DBH distribution pattern of *Litsea grandis*; (d) The basal area distribution pattern of *L. grandis*; (e) The DBH distribution pattern of *Choerospondias axillaris*; (f) The basal area distribution pattern of *C. axillaris*.

Acknowledgements. The authors would like to thank Mr. Niwat Intawin, the members of the Thai Forest Ecological Research Network and students of Forest Biology Department, Faculty of Forestry, Kasetsart University, for their support in field data collection.

Financial support. This research was supported by the Thailand Research Fund in Royal Golden Jubilee (RGJ) Ph.D. Programme (grant number PHD/0216/2558); the National Research Council of Thailand (Project: Biodiversity

Monitoring on the Climate Changes in Huai Kog Ma Biosphere Reserve and adjacent area of Doi Suthep–Pui Mountain Ecosystems, Chiang Mai Province); and Kasetsart University Research and Development Institute, KURDI.

References

Brown JH (2014) Why are there so many species in tropic? *Journal of Biogeography* **41**, 8–22.

- Chen J, Fleming TH, Zhang L, Wang H and Liu Y (2004) Patterns of fruit traits in a tropical rainforest in xishuangbanna, sw china. *Acta Oecologica* **26**, 157–164.
- Corlett R (1998) Frugivory and seed dispersal by vertebrates in the oriental (indomalayan) region. *Biological Reviews* **73**, 413–448.
- Corlett RT (2011) How to be a frugivore (in a changing world). *Acta Oecologica* **37**, 674–681.
- Corlett RT (2014) *The Ecology of Tropical East Asia*. Oxford: Oxford University Press, p. 291.
- Corlett RT (2017) Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: an update. *Global Ecology and Conservation* **11**, 1–22.
- Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG and Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335–380.
- Crausbay SD and Martin PH (2016) Natural disturbance, vegetation pattern and ecological dynamics in tropical Montane forest. *Journal of Tropical Ecology* **32**, 384–403.
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB and Collen B (2014) Defaunation in the Anthropocene. *Science* **345**, 401–406.
- Duengkae P & Marod D (2016) *Study on Role of Frugivory and Seed Dispersal by Vertebrates for Maintain Biodiversity in Hill Evergreen Forest (Research Report)*. Bangkok: Kasetsart University.
- Elliott S and Kuaruksa C (2008) Producing framework tree species for restoring forest ecosystem in northern Thailand. *Small-scale Forestry* **7**, 403–415.
- Fern K (2014) Useful tropical plants database. <http://tropical.theferns.info/>. (Accessed 1 July 2019).
- Flörchinger M and Braun J (2010) Fruit size, crop mass, and plant height explain divergent fruit choice of primates and birds. *Oecologia* **164**, 151–161.
- Forest Botany Division (2016) Concise encyclopedia of plants in Thailand. http://www.dnp.go.th/botany/detail_wordsci.aspx. (Accessed 1 July 2019).
- Gairola S, Rawal RS, Todaria NP and Bhatt A (2014) Population structure and regeneration patterns of tree species in climate-sensitive subalpine forests of India western Himalaya. *Journal of Forestry Research* **25**, 343–349.
- Galetti M, *et al.* (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* **340**, 1086–1090.
- Galetti M, Pizo MA and Morellato LPC (2011) Diversity of functional traits of flesh fruits in a species-rich Atlantic rain forest. *Biota Neotropica* **11**, 181–193.
- Gardner S, Sidisunthorn P and Anusarnsunthorn V (2007) *A Field Guide to Forest Trees of Northern Thailand*. Bangkok: Kobfai Publishing Project, p. 545.
- Gautier-Hion A, Duplantier JM, Quris R, Feer F, Sourd C, Decoux JP, Dubost G, Emmons L, Erard C, Hecketsweiler P, Mougazi A, Roussillon C and Thiolly JM (1985) Fruit characters as a basis or fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* **65**, 324–337.
- Guimarães PR, Galetti M and Jordano P (2008) Seed dispersal anachronisms: rethinking the fruits extinct Megafauna ate. *PLoS ONE* **3**, e1745.
- Harper JL (1977) *Population Biology of Plants*. London: Academic Press, p. 892.
- Herrera CM (1987) Vertebrate-dispersed plants of the iberian peninsula: a study of fruit characteristics. *Ecological Monograph* **57**, 305–331.
- Jordano P (1992) *Fruit and frugivory*. In Ferner M (ed), *Seeds: The Ecology of Regeneration in Plant Communities*. Melksham, UK: Redwood Press Ltd, pp. 105–156.
- Kimura K (2003) A tropical Montane forest in Borneo as a source of fruit supply for frugivorous birds. *Global Environmental Research* **7**, 113–122.
- Kirika JM, Bleher B, Bohning-Gaese K, Chira R and Farwig N (2007) Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. *Basic and Applied Ecology* **9**, 663–672.
- Kitamura S, Yumoto T, Poonswad P, Chuailua, P, Plongmai K, Maruhashi T and Noma N (2002) Interaction between fleshy fruits and frugivores in tropical seasonal forest in Thailand. *Oecologia* **133**, 559–572.
- Larson JE and Funk JL (2016) Regeneration: an overlooked aspect of trait-based plant community assembly models. *Journal of Ecology* **104**, 1284–1298.
- Loiselle BA and Blake JG (2002) *Potential consequences of extinction of frugivorous birds for Shrubs of a tropical wet forest*. In Levey DJ, *et al.* (eds), *Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation*. Wallingford: CABI Publ., pp. 397–406.
- Marod D and Kutintara U (2009) *Forest Ecology*. Bangkok: Faculty of Forestry, Kasetsart University, p. 540.
- Marod D, Sungkaew S, Duengkae P, Asanok L, Kamyo T, Hermhuk S, Panmongkol A and Thinkhampang S (2015) *Plant diversity of lower montane evergreen forest at Huai Kogma watershed area, Doi Suthep-Pui national park, Chiang Mai Province*. In Marod D, Thapjai C (eds), *Proceeding of Thai Forest Ecological Research Network, T-FERN*. Phitsanulok: Narasuan University, pp. 51–60.
- Melese S and Ayele B (2017) Woody plant diversity, structure and regeneration in the Ambo State Forest, South Gonda Zone, Northwest Ethiopia. *Journal of Forestry Research* **28**, 133–144.
- Naniwadekar R, Chaplod S, Datta A, Rathore A and Sridhar H (2019) Large frugivores matter: insights from network and seed dispersal effectiveness approaches. *Journal of Animal Ecology* **88**, 1–13.
- Nathan A and Chee WY (1987) *A Guide to Fruits and Seeds*. Singapore: Singapore Science Centre, p. 144.
- Peña R, Schleunig M, Donoso I, Rodriguez-Perez J, Dalerum F and Garcia D (2020) Biodiversity components mediate the response to forest loss and the effect on ecological processes of plant-frugivore assemblages. *Functional Ecology*. doi: [10.1111/1365-2435.13566](https://doi.org/10.1111/1365-2435.13566).
- R Core Team (2019) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rueangket A, Duengkae P, Thinkhampang S and Marod D (2019) Utilization of fruit by frugivores in lower montane forest at doi suthep-pui national park, Chiang Mai province. *Agriculture and Natural Resources* **53**, 457–464.
- Sekercioglu CH, Daily GC and Ehrlich PR (2004) Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences* **101**, 18042–18047.
- Shanahan M, So S, Compton SG and Corlett R (2001) Fig-eating by vertebrate frugivores: a global review. *Biological Reviews* **76**, 529–572.
- Stiles EW (1989) *Fruit, seeds and dispersal agents*. In Warran GA (ed), *Plant-animal interactions*. United States: McGraw-Hill, pp. 87–122.
- Suzuki S, *et al.* (2007) Fruit visitation patterns of small mammals on the forest floor in a tropical seasonal forest of Thailand. *TROPICS* **16**, 17–29.
- Swamy PS, Sundarapandian SM, Chandrasekar P and Chandrasekaran S (2000) Plant species diversity and tree population structure of a humid tropical forest in Tamil Nadu, India. *Biodiversity and Conservation* **9**, 1643–1669.
- The Botanical Garden Organization (2011) BGO plant database. http://www.qsb.org/Database/BOTANIC_Book%20full%20option/. (Accessed 1 July 2019).
- Tylianakis JM (2013) Ecology. The global plight of pollinators. *Science* **339**, 1532–1533.
- Valenta K and Nevo O (2020) The dispersal syndrome hypothesis: how animals shaped fruit traits, and how they did not. *Functional Ecology* **2020**, 1–12.
- Valido A, Schaefer HM and Jordano P (2011) Colour, design and reward: phenotypic integration of fleshy fruit displays. *Journal of Evolutionary Biology* **24**, 751–760.
- Van der Pijl L (1982) *Principle of Seed Dispersal in Higher Plants*. Berlin: Springer-Verlag, p. 153.
- Vander Wall SB (2001) The evolutionary ecology of nut dispersal. *The Botanical Review* **67**, 74–117.
- Vander Wall SB (2010) How plants manipulate the scatter-hoarding behavior of seed-dispersing animals. *Philosophical Transactions of the Royal Society B* **365**, 989–997.
- Vongkuna K (2005) *Diversity of epiphytic mosses at Huay Kog Ma Doi Suthep-Pui Chiang Mai Province*. MS Thesis, Thailand: Chiangmai University.
- Wheelwright NT (1985) Fruits size, gape width, and the diets of fruit-eating birds. *Ecology* **66**, 808–818.
- Wheelwright NT and Janson CH (1985) Colors of fruit displays of bird-dispersed plants in two tropical forest. *American Naturalist* **126**, 777–799.