Population Structure and Spatial Distribution of Tree Species in Lower Montane Forest, Doi Suthep-Pui National Park, Northern Thailand

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ABSTRACT

Plant diversity is important for sustainable development, particularly in watershed areas. This study explored tree population and diversity in a lower montane forest (LMF). A 16-ha permanent plot was established in LMF at Huai Kogma sub-watershed, northern Thailand. All trees with a diameter at breast height ≥ 2 cm were tagged, measured, identified, and their coordinates were mapped. The results showed that 220 species in 139 genera from 63 plant families were found. The dominant families based on species numbers and tree density were Fagaceae, Lauraceae, and Theaceae. The most dominant species were *Castanopsis acuminatissima*, *Schima wallichii*, *Castanopsis armata*, and *Styrax benzoides*. Diameter classes for climax species frequently followed negative exponential distributions, indicating their populations could be maintained into the future. By contrast, pioneer species, such as *Macaranga indica*, *Morus macroura*, and *Rhus javanica*, had discontinuous distribution, and were mostly found in gap areas, indicating successful regeneration may require high light intensity. Spatial distribution patterns based on Morisita's index showed that most of the selected species had clumped patterns, particularly those in the Fagaceae family, which were predominantly distributed along the mountain ridge. Tree distribution patterns can affect ecological dynamics, thus reinforcing patterns dependent on local interactions such as the abundance of and distance to available resources. Our finding can aid evaluations of forest sustainability, and support the biodiversity conservation plans. In particular, the selection of suitable species for LMF restoration programs where mixed plantings of pioneer and climax species are planned.

1. INTRODUCTION

Understanding how species are distributed, and how they assemble to form communities and ecosystems, is an important issue that has attracted considerable scientific interest. Its information is a very useful component of conservation and management decisions, including focused efforts to conserve rare species, habitat management and restoration, anticipation of problematic invasions, and delimit valued habitat types (Franklin, 2010).

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Vegetation ecologists have engaged in an extended debate on the mechanisms governing species assemblage into complex vegetation communities (Ricklefs, 2008; Brooker et al., 2009). Ongoing global changes, including climate change, deforestation, pollution, and biological invasions, have increased rates of biodiversity loss (Cardinale et al., 2012; Chen et al., 2011; Pereira et al., 2010; Sala et al., 2000). These changes have also heightened the need for knowledge that could help us anticipate and prevent deleterious effects on biodiversity and ecosystem functioning. This is especially important for mountain ecosystems, which are particularly exposed to climate changes (Pepin et al., 2015), and life mainly temperature limited and vulnerable to climatic changes (Amdre et al., 2009).

Mountain ecosystems are mainly defined in terms of their minimum altitude in meters above sea level (m.a.s.l.), which ranges from 300 m at 67°N and 55°S to 1,000 m at the equator. Mountain ecosystems cover about 27% of the Earth's surface (Kapos et al., 2000). They maintain ecological processes and services for both mountain communities and those living in lowlands, wherein demand from population centers, agriculture and industry is high (Regato and Salman, 2008). Mountains are exposed to both natural and anthropogenic drivers of change (Kampmann et al., 2008). In particular, montane plant diversity can be reduced by certain types of land-use, including intensification and land abandonment (Spehn et al., 2006). Mountain biota are adapted to extreme climatic conditions, temperatures, and precipitation (Rashid et al., 2005). Recovery of mountain ecosystems from disturbances is typically slow.

The characteristics of montane forests differ from those of lowland forests due to changes in vegetation composition along the altitudinal gradient (Marod et al., 2014; Richards, 1996). It is now accepted that four forest zones exist for taller tropical mountains up to the tree line, namely lowland, lower montane, upper montane and subalpine forest zones (Ashton, 2003). The transition from lowland to lower montane forest (LMF) seems to be mostly attributable to declining average temperature with elevation. At this threshold, many lowland tree species are displaced by a floristically distinct assemblage of montane species (Kitayama, 1992). Tree species from the Fagaceae and Lauraceae are particularly abundant in massifs, where their abundance in both the canopy and subcanopy has earned these forests the name "oak-laurel forests" (Tagawa, 1995).

Only two mountain forest ecosystems are found in Thailand: the LMF and upper montane forest (UMF). The ecotone between them is located at approximately 1,800 m.a.s.l. based on climatic characteristics and edaphic conditions (Santisuk, 1988). Mount Doi Inthanon, at 2,565 m.a.s.l., is a summit in Thailand with extensive tracts of UMF. Trees are often small in stature and characterized by umbrella-shaped crowns, small leaves, gnarled stems, and branches that are covered by epiphytes such as orchids, ferns, lichens, and mosses (Hara et al., 2002; Khamyong et al., 2004). Several studies have reported that species from the Fagaceae and Lauraceae families are the most abundant, as also seen in tropical mountain forest areas (Kanzaki et al., 2004; Marod et al., 2018; Sri-Ngernyuang et al., 2003).

Intensive studies of species composition, forest structure, and dynamics have been conducted in lowland forests since the 1980s using large-scale research plots (Condit, 1995). Large-scale research plots are not only suitable for studying the distribution patterns of existing trees, but also tree regeneration, which is often expressed in terms of stem-size distributions (Bunyavejchewin et al., 2001; Kanzaki et al., 2004; Yamada et al., 1997). Diameter class distributions (visualized using graphs showing the density of trees in several different classes) can be used to determine whether the density of smaller trees in a forest is sufficient to replace the current population of larger trees (Henle et al., 2004; Rubin et al., 2006; White et al., 2007). Whether a given forest is "sustainable" can be inferred from stand diameter distributions. For example, in the absence of major disturbances, a reversed J-shaped distribution in uneven-aged stands has been regarded as demonstrating dynamic equilibrium in sustainably managed forests (Marod et al., 2020; Nyland, 2002). Unimodal distributions characterized by fewer juveniles relative to adults have been interpreted as evidence of population decline (Condit et al., 1998; Deb and Sundriyal, 2008). The success of regeneration efforts can also be inferred from diameter distribution patterns associated with ecological processes. Distribution patterns (clumped or grouped, and regular or random) can effect ecological changes depending on local interactions among individuals, seed dispersal and germination, abundance, and ecological niche.

Measuring distribution patterns and linking them to ecological processes is an ongoing area of ecological research. The Morisita Index of aggregation (I_δ) can be used to measure and interpret spatial point patterns (Golay and Kanevski, 2015). This index measures whether a given point pattern is clumped or dispersed relative to a spatially random distribution. The value taken by the index depends on both quadrat size and population density. The Morisita Index has been applied to detect distribution patterns and understand the processes of seed dispersal, seed banking, and tree establishment (De Almeida and Galetti, 2007; Houle, 1994). It has also been used to analyze spatial patterns of regeneration and adult tree distributions (Hubbell, 1979). These data can help us estimate forest sustainability based on population structure and regeneration status. Thus, this study aimed to clarify the population structure and regeneration status of tree species in an area of LMF, and the relative distribution patterns of sapling-, pole-, and adult-stage tree in a 16-ha permanent plot in an LMF.

2. METHODOLOGY

2.1 Study site

The Kog Ma sub-watershed (18°48′N, 98°54′E) is one of the Mae Sa head-watersheds which is located on the east-facing slope of Mount Doi Pui (1,685 m.a.s.l.), 10 km west of Chiang Mai Province in northern Thailand (Figure 1). The sub-watershed area is 0.65 km^2, and covered by primary LMF with canopy heights of 25-40 m. The dominant tree species are predominantly members of the Fagaceae, especially the genera *Castanopsis*, *Lithocarpus*, and *Quercus*, together with a variety of undergrowth, shrub, and epiphytic species (Bhumibhamon and Wasuwanich, 1970). Many hydrological studies were found in several aspects (Kume et al., 2007; Tanaka et al., 2003; Tanaka et al., 2008). However, because less documentation on forest structure and dynamics of LMF has been reported, particularly based on a large permanent plot, an evaluation of LMF was selected for this study. The climate is subtropical, and the wet season (May to October) transitions to a cool dry season (November to January) and subsequent hot dry season (February to April). The mean annual temperature and rainfall are 20°C and 1,700 mm, respectively. The majority of precipitation occurs in the wet season, with only about 8% of the annual total falling during the dry season (Kume et al., 2007; Tangtham, 1974). The soils are classified as reddish-brown laterites (Thailand soil classification) or Ultisols (USDA Soil Taxonomy), with about 50% sand content and 60-74% porosity (Hashimoto, 2005).

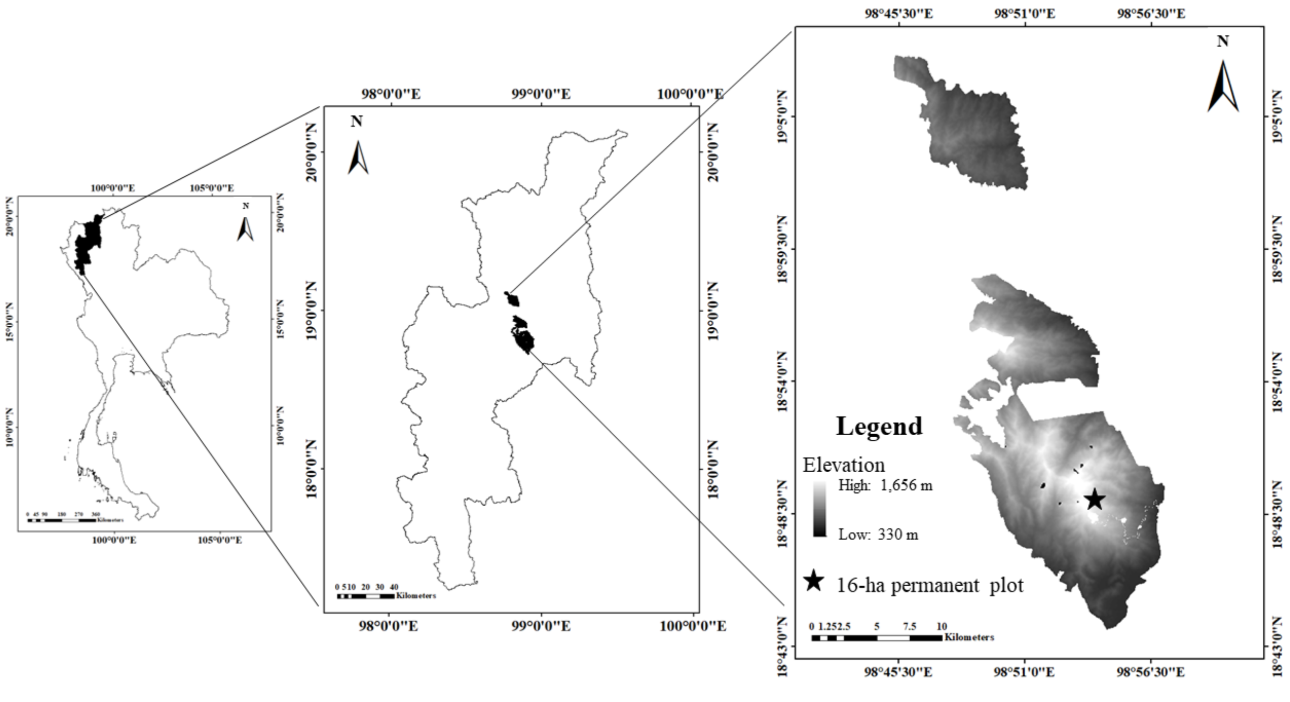


Figure 1. Study area with a 16-ha plot (★) in LMF at Doi Suthep-Pui National Park, northern Thailand

2.2 Data collection

Large permanent plots are widely used to monitor tree spatial distribution and population dynamics relating to the environmental changes (Condit et al., 2000). In 2010, a 16-ha permanent plot was established at an elevation range from 1,300-1,450 m.a.s.l. The plot measured 400 m × 400 m and was subdivided into 1,600 10 m × 10 m subplots to study forest structure and species composition based on Condit et al. (2014). All trees with a diameter at breast height (DBH, 1.3 m above the soil surface) of ≥2 cm were tagged with a running number, measured, and identified to species. Tree coordinates (x, y) in each subplot were also recorded. Leaf specimens were collected from the enumerated trees and identified by referring to herbarium specimens at the Forest Herbarium of Department of National Parks, Wildlife and Plants Conservation. Species nomenclature was based on Smitinand (2014).

2.3 Data analysis

Plant ecological indices were calculated to clarify the forest structure. For all stems with a DBH ≥ 5.0 cm, the density, dominance and importance value index (IVI) were calculated based on the sum of relative density, dominance and frequency (Krebs, 1994). Basal area (BA), density and diversity were also calculated for each plant family by summing these variables across all species in a given family. The size class distribution for all species with at least 30 individuals in the 16-ha plot were prepared. This analysis included the small size class of saplings (2.0 ≤ DBH < 5.0 cm). The population structure across this size reflects that of larger trees (Mclaren et al., 2005). Size class distribution of each species was defined by families of probability mass functions fitting to the class frequency. In order to specifically select the most suitable family of mass distribution, Anderson-Darling statistic (Anderson and Darling 1952; Liebscher, 2016) and probability-probability plot (Chambers et al., 2017) were then applied to help determine the goodness-of-fit among families of the probability function. Subsequently, the optimal probability function was specified from the set of the distribution function (varied number of parameters) of the selected family using the Likelihood ratio test and Akaike Information criteria (Akaike, 1998). The regeneration status of each tree species was predicted on the basis of its size-class distribution.

To detect the distribution patterns of saplings, pole-stage (5.0 ≤ DBH < 10.0 cm) and mature trees (DBH ≥10.0 cm), all species with >80 individuals were selected (Lan et al., 2009). Morisita's I_δ index was calculated by dividing the plot into quadrats of various sizes. The smallest quadrat size was obtained by dividing the 16-ha plot into square quadrats each with a size of $(0.1)^2$ m × 400 m (i.e., x-axis length) and $(0.10)^2$ × 400 m (i.e., y-axis length), yielding 4 m × 4 m (16 m^2) quadrats. Larger quadrats were obtained by doubling the length of the smaller quadrats, producing quadrats that ranged from 16 m^2 to 6.5 ha. Morisita's I_δ was then calculated using the following equation (Morisita, 1959):

$$I_\delta = q\,\frac{\sum n_i^2 - N}{(N^2 - N)}$$

Where; n_i is the number of individuals in each quadrat, N is the total number of individuals in the16 ha plot, and q is the number of quadrats of a given size.

The I_δ value was used to classify distribution patterns as random (I_δ=1), clumped or aggregated (I_δ >1), or regular (I_δ <1). F-tests were used to test for departures from random expectation for each quadrat size. The statistical significance of the F-tests was tested at the 95% confidence limit ($p<0.05$).

3. RESULTS AND DISCUSSION

3.1 Species composition and population structure

A total of 28,078 individuals ≥2 cm DBH were measured and identified. This population was composed of 220 species from 139 genera and 63 families. The average density of all trees ≥5.0 cm DBH was 806.88 stems/ha, and this population included 195 species from 131 genera and 56 families (Table S1). The highest tree density (stems/ha) was found for *Castanopsis acuminatissima* (n=106.56) followed by *Styrax benzoides* (n=38.94), *Vernonia volkameriiolia* (n=36.19), *Castanopsis armata* (n=29.00), *Litsea martabanica* (n=27.31), *Persea gamblei* (n=24.81), *Helicia nilagirica* (n=22.44), *Turpinia pomifera* (n=20.06), and *Schima wallichii* (n=19.13). A number of other temperate tree species were present in low densities, including members of the families Podocarpaceae (*Podocarpus neriifolius* and *Dacrycarpus imbricatus*), Betulaceae (*Betula alnoides* and *Carpinus viminea*), and Juglandaceae (*Engelhardtia spicata* and *E. serrata*). The most dominant tree species, with an average BA of 32.79 m^2/ha and relative basal area (RBA, %) of 14.24, was *Castanopsis acuminatissima*. Other dominant species were *Schima wallichii* (RBA=9.23%), *Manglietia garrettii* (6.41%), *Castanopsis armata* (5.36%), *Castanopsis tribuloides* (4.80%), *Litsea grandis* (3.15%), *Syzygium toddlioides* (2.89%), *Syzygium tetragonum* (2.87%), *Choerospondias axillaris* (2.81%), and *Michelia baillonii* (2.24%). These 10 species accounted for 54.00% of the total BA. To determine the ecological influence of each species, the IVI (%) was calculated. The species with the highest IVI was *Castanopsis acuminatissima* (33.36), followed by *Schima wallichii* (14.61), *Castanopsis armata* (12.86), *Styrax benzoides* (9.55), *Castanopsis tribuloides* (8.85), *Litsea martabanica* (8.29), *Manglietia garrettii* (8.23), *Persea gamblei* (8.20), *Vernonia volkameriiolia* (6.21), *Litsea martabanica* (7.45), *Helicia nilagirica* (6.30), and *Syzygium toddlioides* (6.21).

The Euphorbiaceae, Lauraceae, Fagaceae, Moraceae, and Theaceae families had the most species (20, 19, 16, 11, and 8 species, respectively). The Fagaceae family had the highest per hectare tree density (186.31 stems/ha) followed by the Lauraceae (92.69 stems/ha), Euphorbiaceae (71.00 stems/ha), Theaceae (39.69 stems/ha), and Styracaceae (38.94 stems/ha) families. The Fagaceae family also had the highest BA (9.69 m^2/ha), followed by the Lauraceae (4.11 m^2/ha), Theaceae (3.40 m^2/ha), Magnoliaceae (2.76 m^2/ha), and Myrtaceae (2.38 m^2/ha) families (Figure 2).

As also reported for tropical montane forests elsewhere in Southeast Asia (Brambach et al., 2017; Buot and Okitsu, 1998; Maxwell et al., 1997; Ohsawa, 1995; Pendry and Proctor, 1997), the Fagaceae and Lauraceae families were more abundant and more likely to occupy the highest layer of the tree canopy in the LMF in this study. The name "oak-laurel forest" has been used for this vegetation type (Ashton, 2003; Kochummen, 1989). Oak-laurel forests are the dominant vegetation type in the mountains of tropical Asia from the Himalayas to New Guinea (Sri-Ngernyuang et al., 2003), and are closely related to the temperate evergreen oak forests of East Asia (Tagawa 1995; Zhu et al., 2016). However, in Malesia, tropical lower montane forests are often dominated more by Myrtaceae than by Lauraceae (Aiba and Kitayama, 2020; Kochummen, 1982). Ashton (2015) reported that lower-montane oak-laurel forest is rare in Borneo and patchy in Peninsular Malaysia, and he named lower montane forest on Mount Mulu, Borneo, as "lower montane kerangas". A similar name for lower montane forest on old soil with low dominance of Lauraceae at Mount Kinabalu has also been mentioned (Aiba and Kitayama, 2020).

3.2 Regeneration of tree species

The characteristics of regenerating tree populations were explored using DBH-class distributions. In total, 123 tree species with populations comprising >30 individuals were analyzed. The result showed that DBH classes followed two distributions: negative exponential (NE; reverse-J) and polynomial (PO). Size class distributions for 78 species followed an NE distribution. These distributions have the greatest numbers of individuals in the lowest DBH class and progressively fewer individuals in larger DBH classes (Table S1). Considering the dominance of the Fagaceae, only three species from that family - *Castanopsis acuminatissima*, *C. tribuloides*, and *Lithocarpus truncates* - followed NE distributions (Figure 3 (a)-(c)); this indicated that they had a robust capacity to maintain a stable population structure in the future, because smaller trees will grow into larger size classes and thus replace larger trees as they die. In particular, these species would be sustained if mortality were greater among small (suppressed) trees and large trees than among mid-sized co-dominants

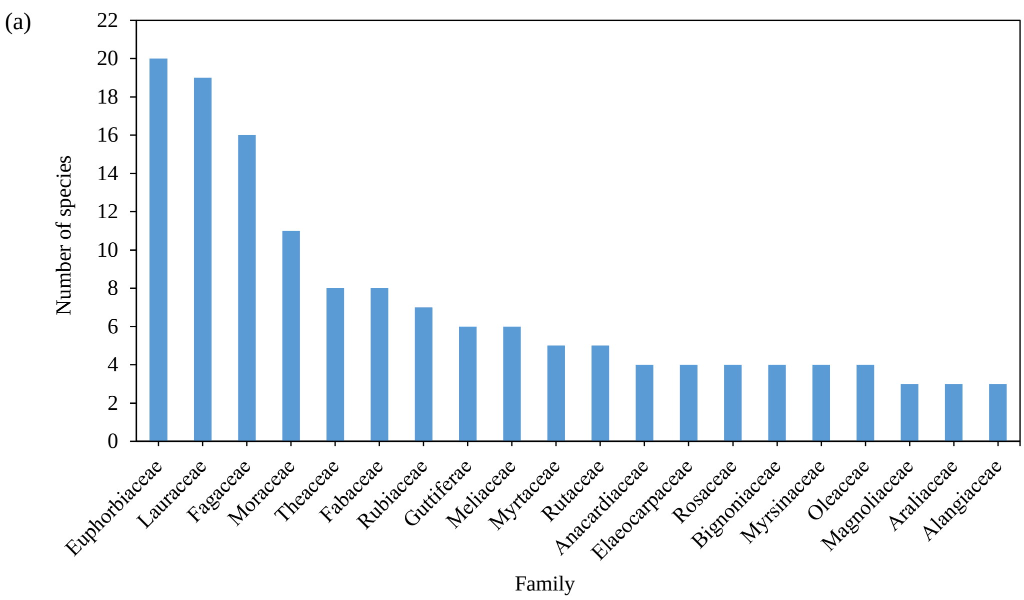


Figure 2. (a) Numbers of species, (b) tree densities, and (c) basal areas of the 20 most dominant families in the LMF for stems ≥ 5.0 cm DBH

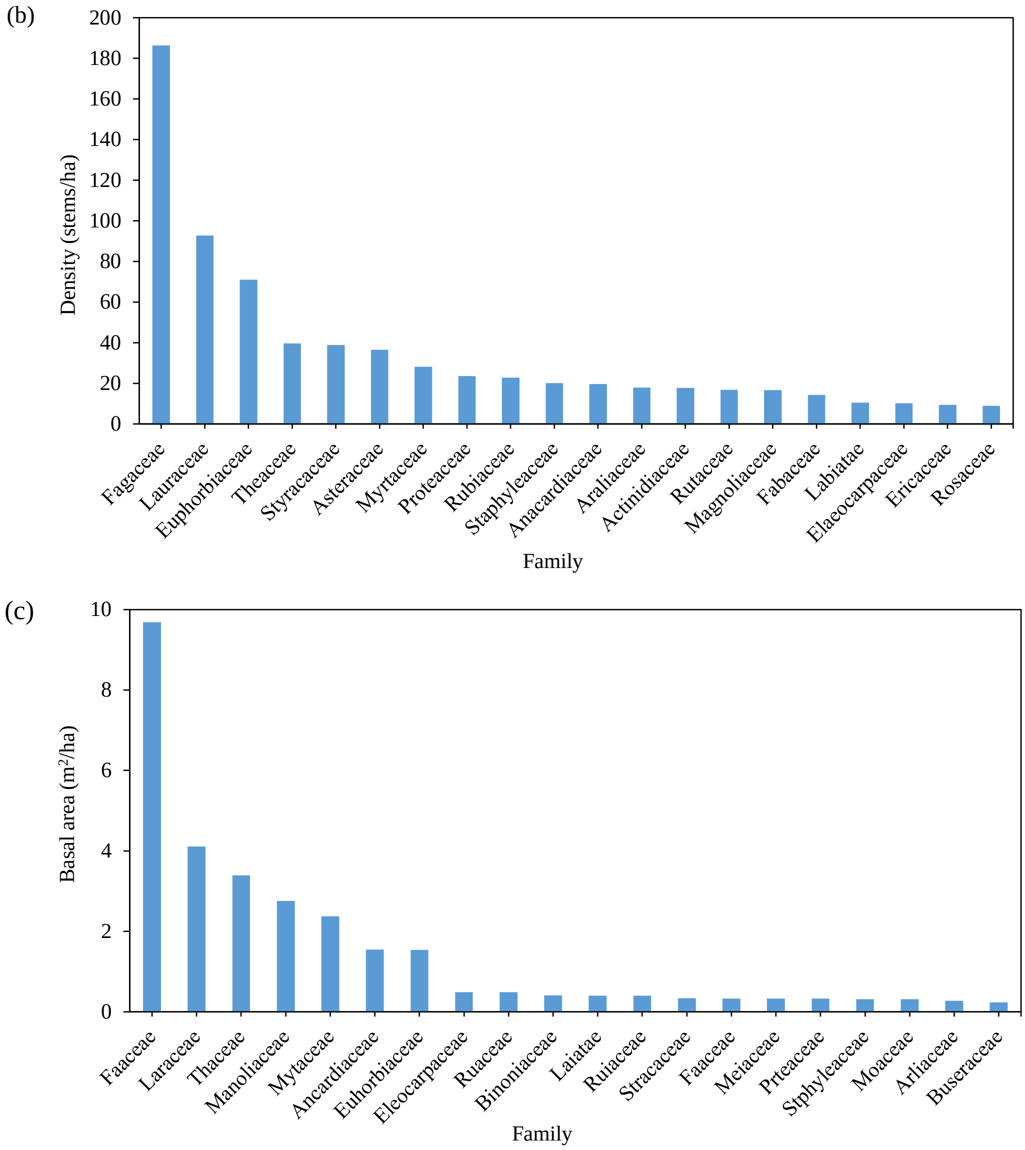


Figure 2. (a) Numbers of species, (b) tree densities, and (c) basal areas of the 20 most dominant families in the LMF for stems ≥5.0 cm DBH (cont.)

(Goff and West, 1975). Other species belonging to the Fagaceae followed PO distributions, in which discontinuous DBH class distributions were detected (Figure 3 (d)-(h)). A lack of successful regeneration could have been caused by the activities of seed predators or frugivores, particularly small rodents that eat the seeds of Fagaceae (Rueangket et al., 2019). The large, edible seeds of *C. diversifolia* and *C. armata* were overexploited by local people, leading to reduced seed germination and discontinuous size-class distributions. Forty-six species followed PO distributions. Most species of Lauraceae, including *Actinodaphne henryi*, *Cinnamomum inner*, and *Litsea pierrei*, had discontinuous size-class distributions expressed through PO curves (Table S1).

Pioneer species, such as *Macaranga indica*, *Morus macroura*, *Erythrina subumbrans*, and *Rhus javanica* (Figure 4 (a)-(d)), also followed PO distributions. The late pioneer species, *Choerospondias axillaris*, *Schima wallichii*, and *Betula alnoides*, showed the same patterns (Figure 4 (e)-(g)). Pioneer species were mostly found in canopy gaps, which suggests that bright light conditions in disturbed areas are required for their successful establishment (Goodale et al., 2012; Huth and Wagner, 2006; Miyazawa et al., 2006; Sangsupan et al., 2021; Swinfield et al., 2016).

One of the conifer species, *Podocarpus neriifolius*, had a low population density of eight trees with DBH >10 cm in the whole 16-ha plot. Similarly low densities (2-4 trees/ha of DBH >10 cm) of this species were found in montane forests in Papua New Guinea (Enright and Jaffré, 2011). Its regeneration may be unable to compete with angiosperms or rainforest tree species that can absorb light as seedlings in a shaded understory, but which rapidly increase their growth rates when light availability increases (Brodribb et al., 2012; Wright et al., 2010). Therefore, we cautiously conclude that diameter distributions can indicate whether the density of smaller trees in a stand is sufficient to replace the current population of larger trees, which may help us to estimate forest sustainability.

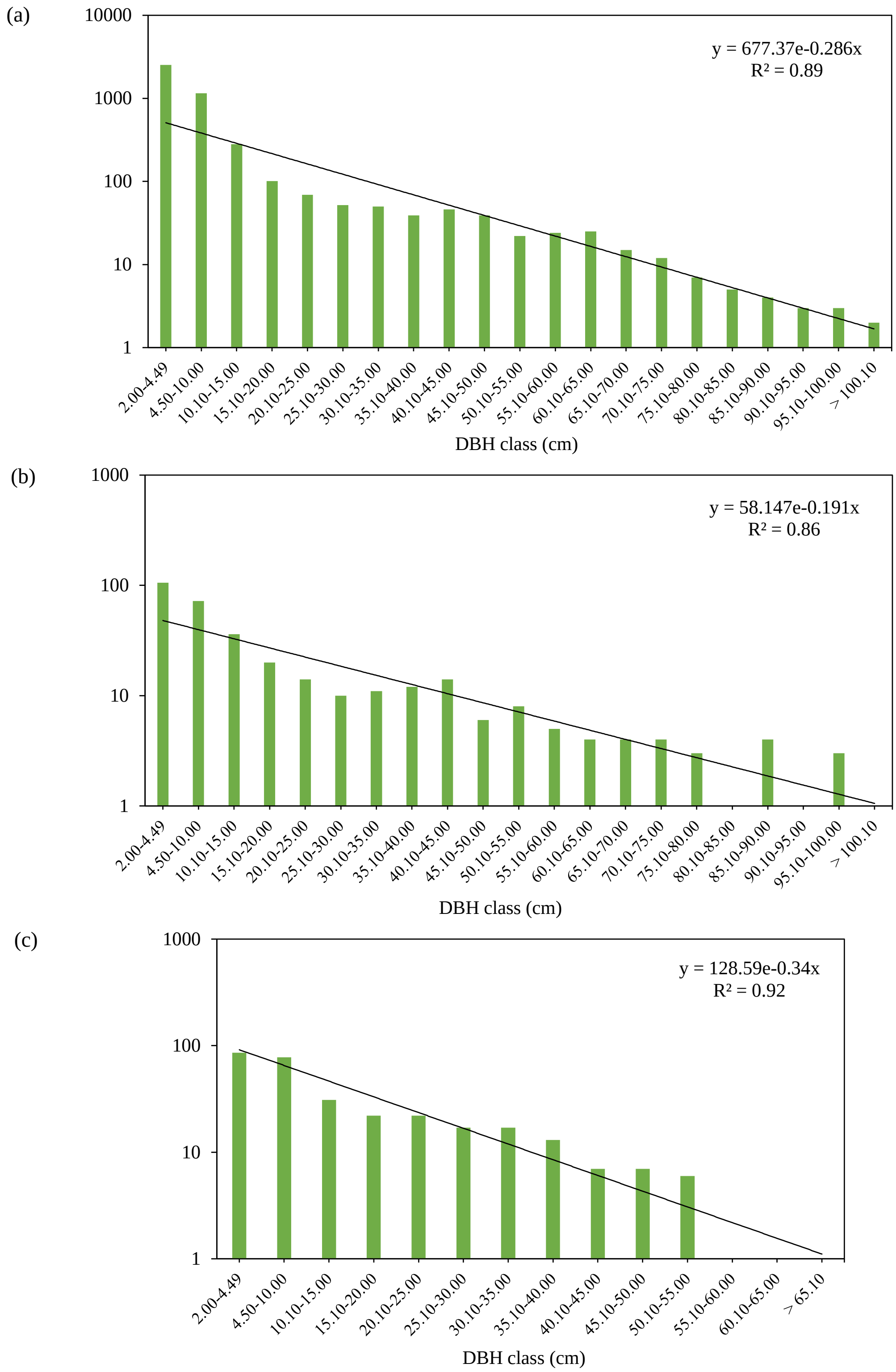
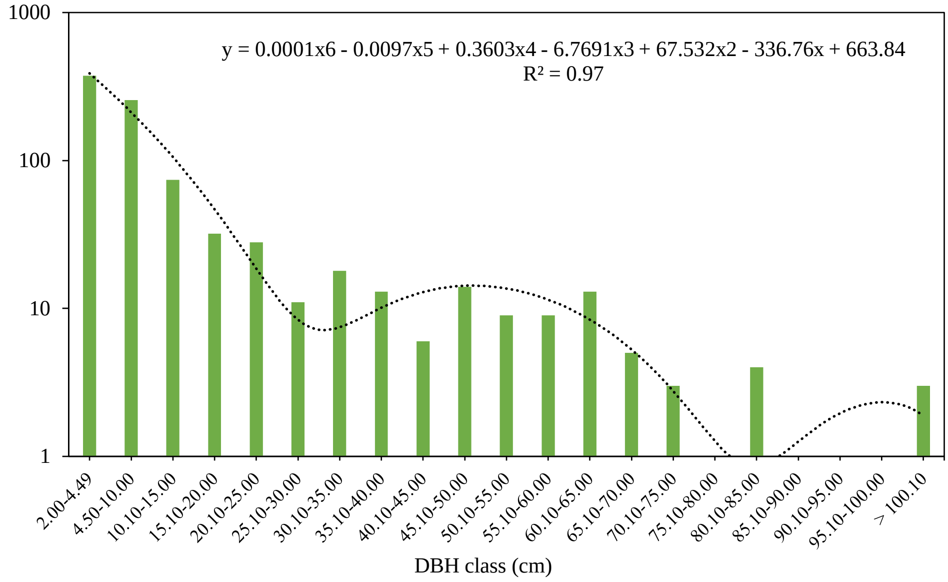
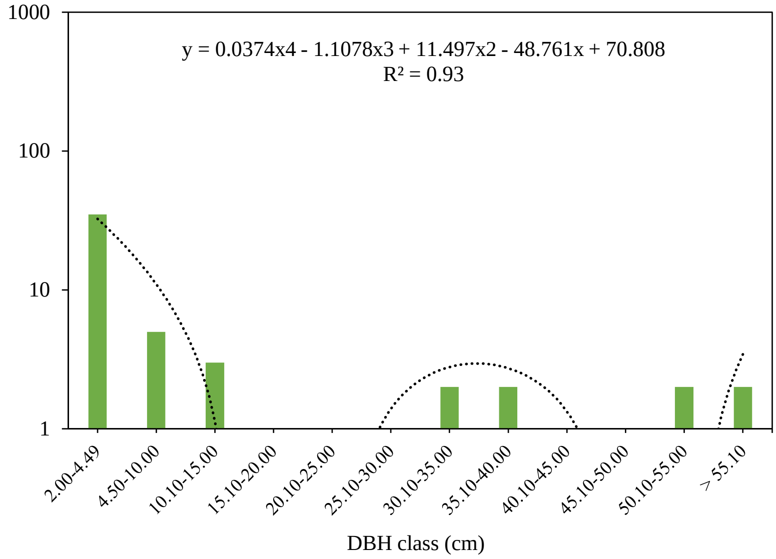


Figure 3. Diameter class distributions plotted on a logarithmic scale for some species of Fagaceae. (a) *Castanopsis accuminatissima*, (b) *Castanopsis tribuloides*, (c) *Lithocarpus truncatus*, (d) *Castanopsis armata*, (e) *Castanopsis diversifolia*, (f) *Castanopsis argyrophylla*, (g) *Lithocarpus mekongensis*, and (h) *Lithocarpus auriculatus*

(d)



(e)



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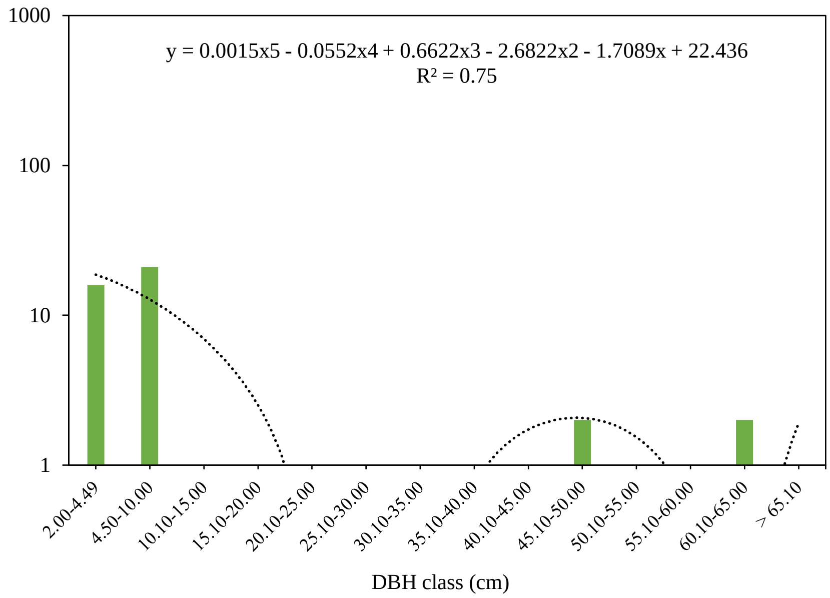

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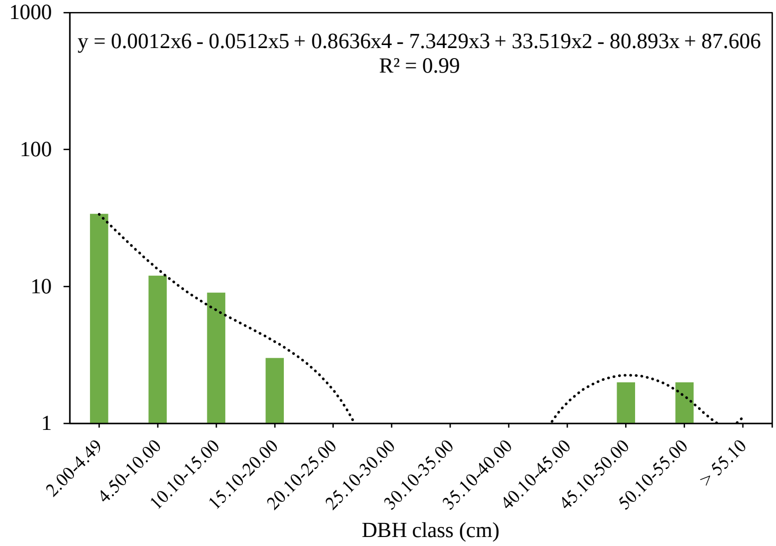
(g)



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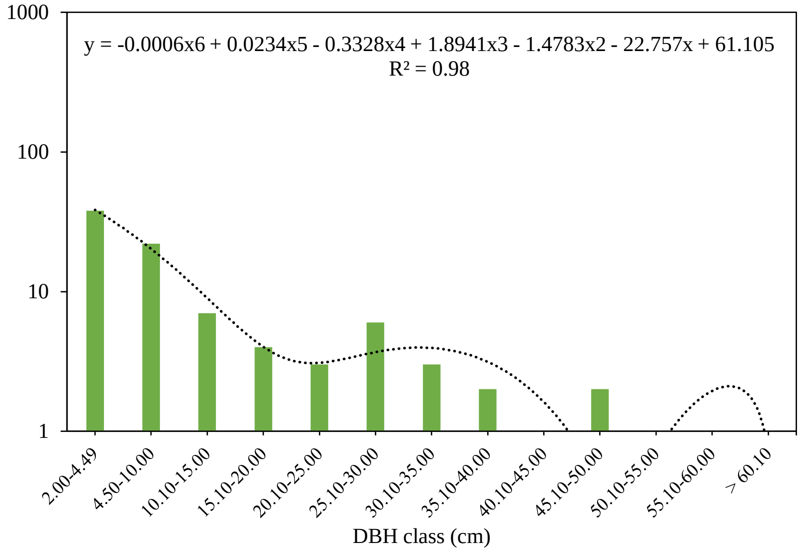

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(a)

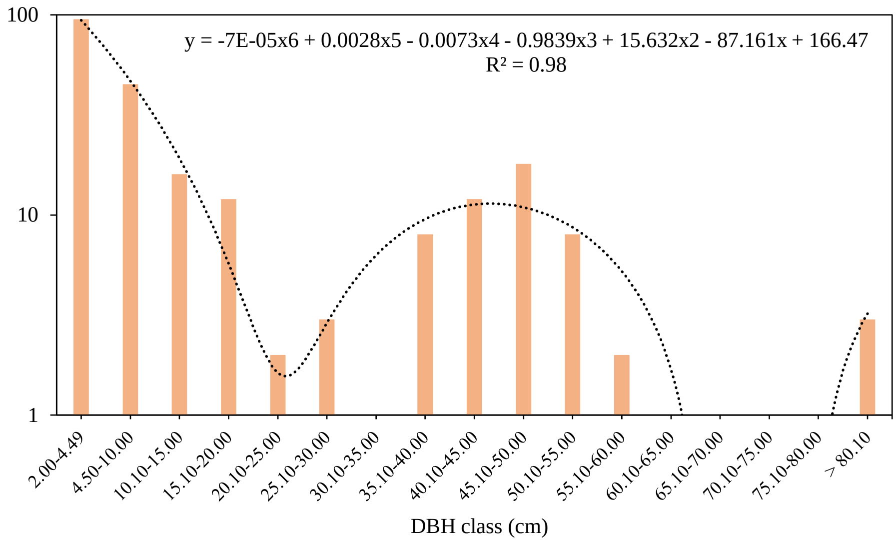
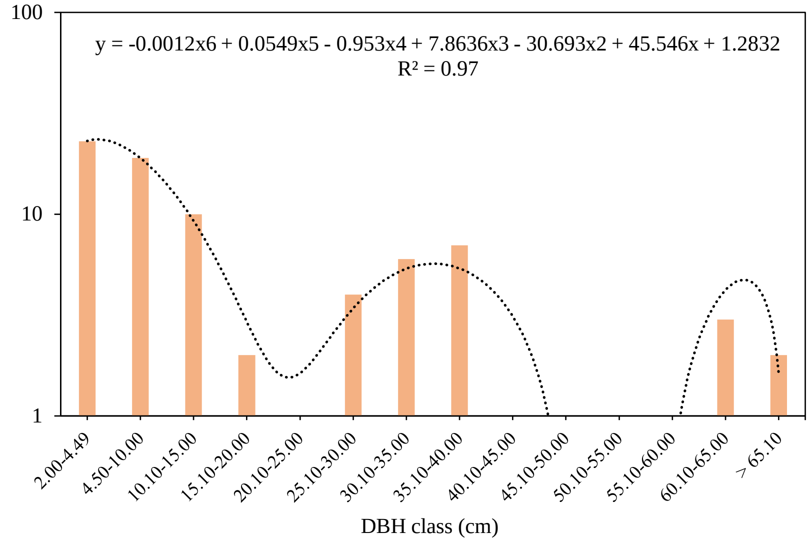


Figure 4. Diameter class distributions plotted on a logarithmic scale for pioneer species: (a) *Macaranga indica*, (b) *Morus macroura*, (c) *Erythrina subumbrans*, (d) *Rhus javanica*, (e) *Choerospondias axillaris*, (f) *Schima wallichii*, (g) *Betula alnoides*, and the shade-tolerant species as (h) *Podocarpus neriifolius*

(b)



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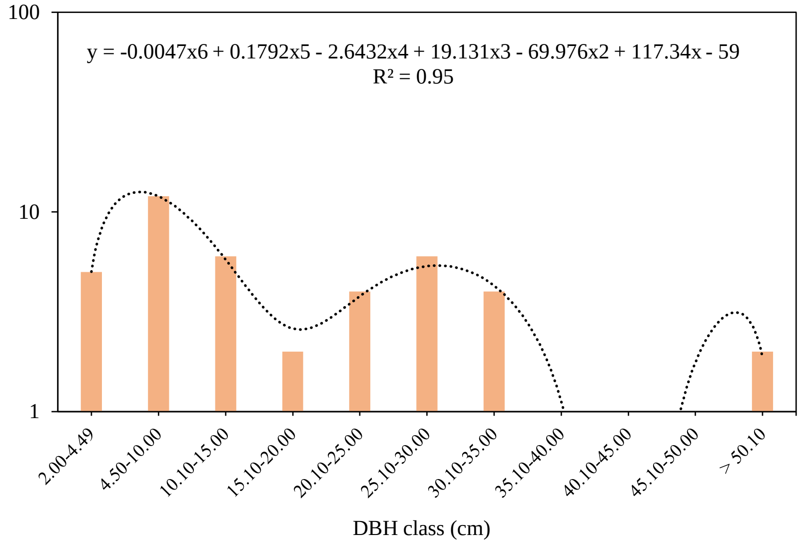

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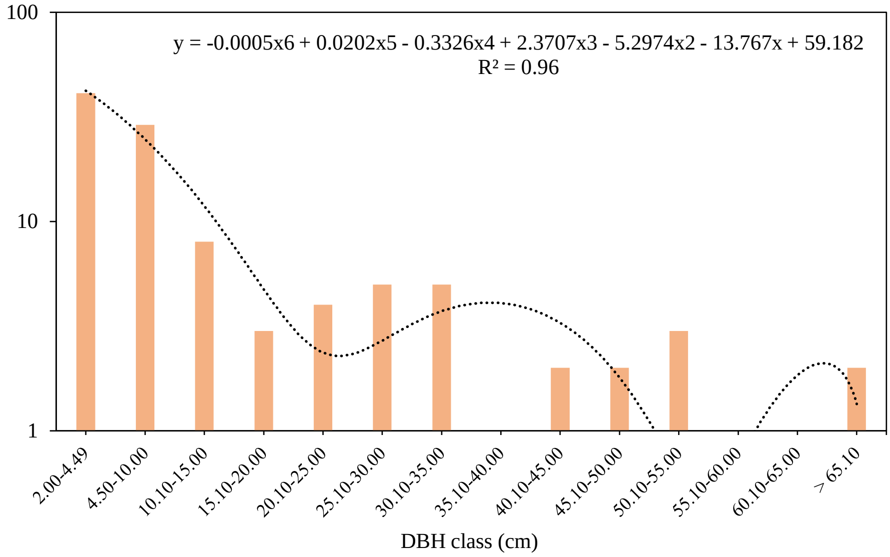

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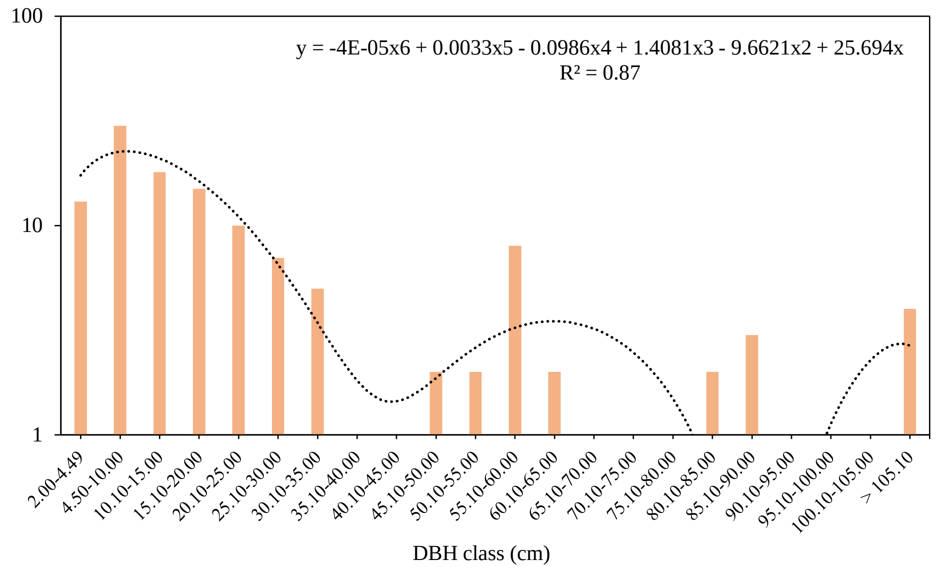
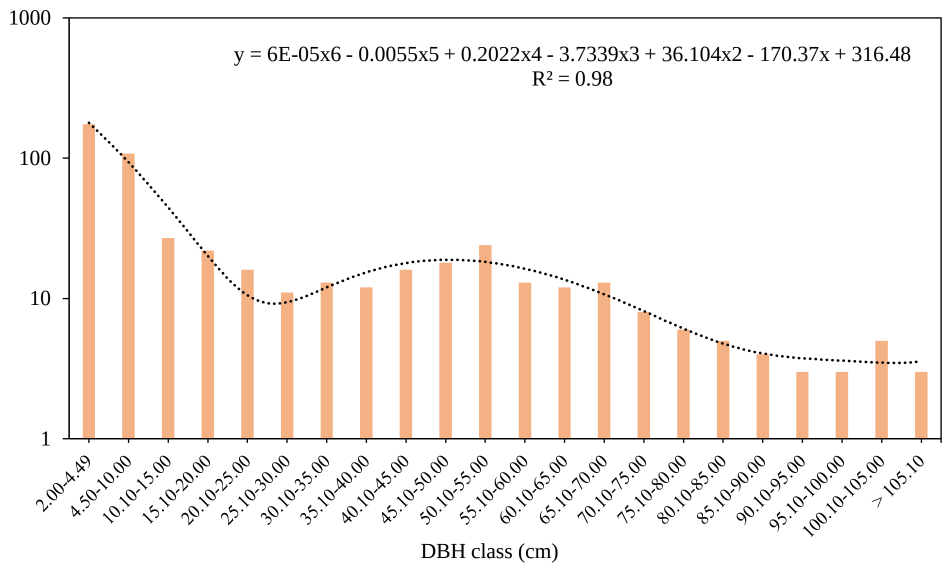
(e)



(f)



(g)

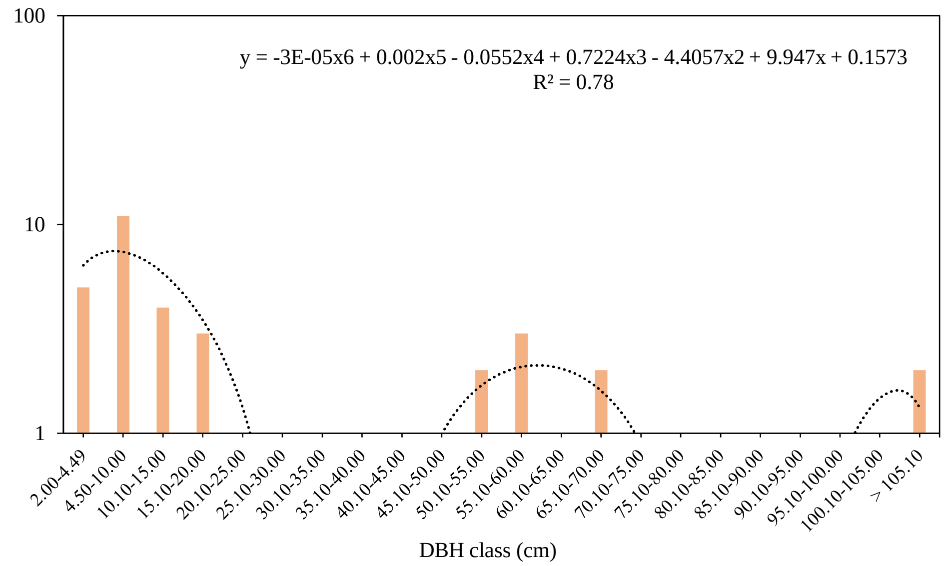


Figure 4. Diameter class distributions plotted on a logarithmic scale for pioneer species: (a) *Macaranga indica*, (b) *Morus macroura*, (c) *Erythrina subumbrans*, (d) *Rhus javanica*, (e) *Choerospondias axillaris*, (f) *Schima wallichii*, (g) *Betula alnoides*, and the shade-tolerant species as (h) *Podocarpus neriifolius* (cont.)

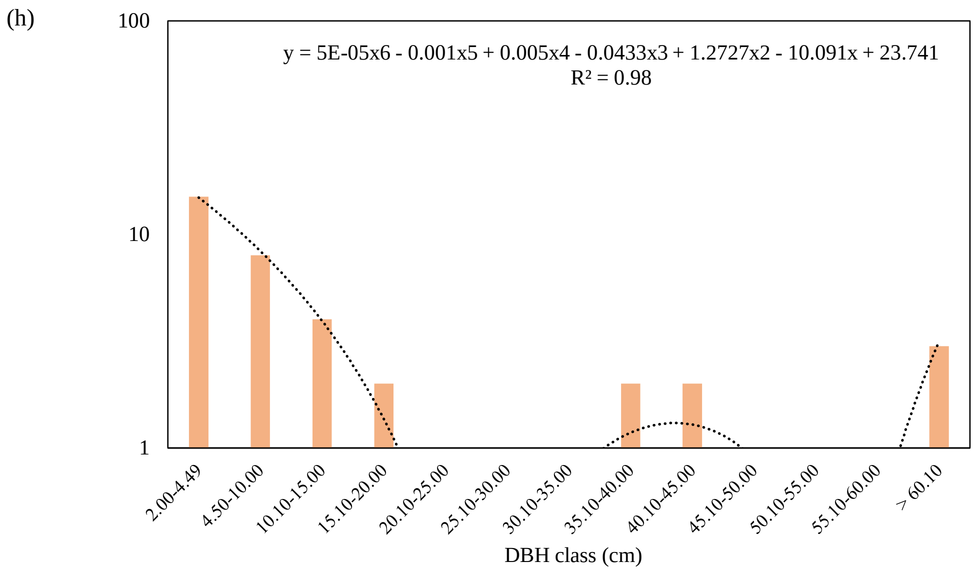
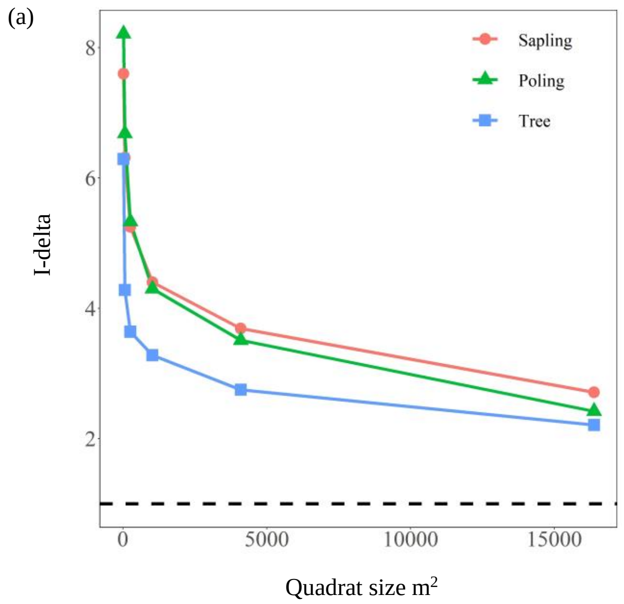


Figure 4. Diameter class distributions plotted on a logarithmic scale for pioneer species: (a) *Macaranga indica*, (b) *Morus macroura*, (c) *Erythrina subumbrans*, (d) *Rhus javanica*, (e) *Choerospondias axillaris*, (f) *Schima wallichii*, (g) *Betula alnoides*, and the shade-tolerant species as (h) *Podocarpus neriifolius* (cont.)

3.3 Tree distribution pattern

Seventy-two species were selected for the analysis of spatial distribution patterns. The Morisita index, I_δ, varied among species, growth stages (sapling, pole stage, and mature tree) and quadrat sizes. As quadrat size increased, the intensity of spatial aggregation decreased. Sixty-two species had clumped patterns ($I_\delta > 1.0$) for all growth stages and quadrat sizes (Table S1). Aggregated spatial patterns were particularly observed in dominant Fagaceae species, such as *Castanopsis acuminatissima*, *C. armata*, and *Lithocarpus truncatus* (Figure 5). *Manglietia garrettii*, *Prunus arborea*, *Bridelia glauca*, *Markhamia stipulate*, and *Lithocarpus dealbatus* followed random patterns as saplings, but were clumped as pole-stage and mature trees (Figure 6). By contrast, *Michelia baillonii*, *Schima wallichii*, *Canarium euphyllum*, and *Elaeocarpus serratus* were clumped as saplings but randomly distributed in other life stages (Figure7). Only one species, *Tarennoidea wallichii*, had a random spatial pattern at every growth stage (Figure 7(d)).



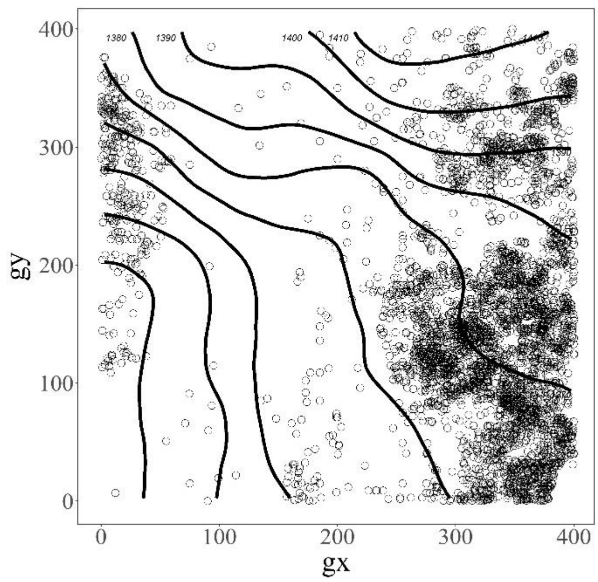


Figure 5. Clumped spatial distribution patterns of dominant Fagaceae at each growth stage in the 16-ha permanent plot at HKM: (a) *Castanopsis accuminatissima*, (b) *C. armata*, (c) *Lithocarpus truncatus*, and (d) *Quercus oidocarpa*

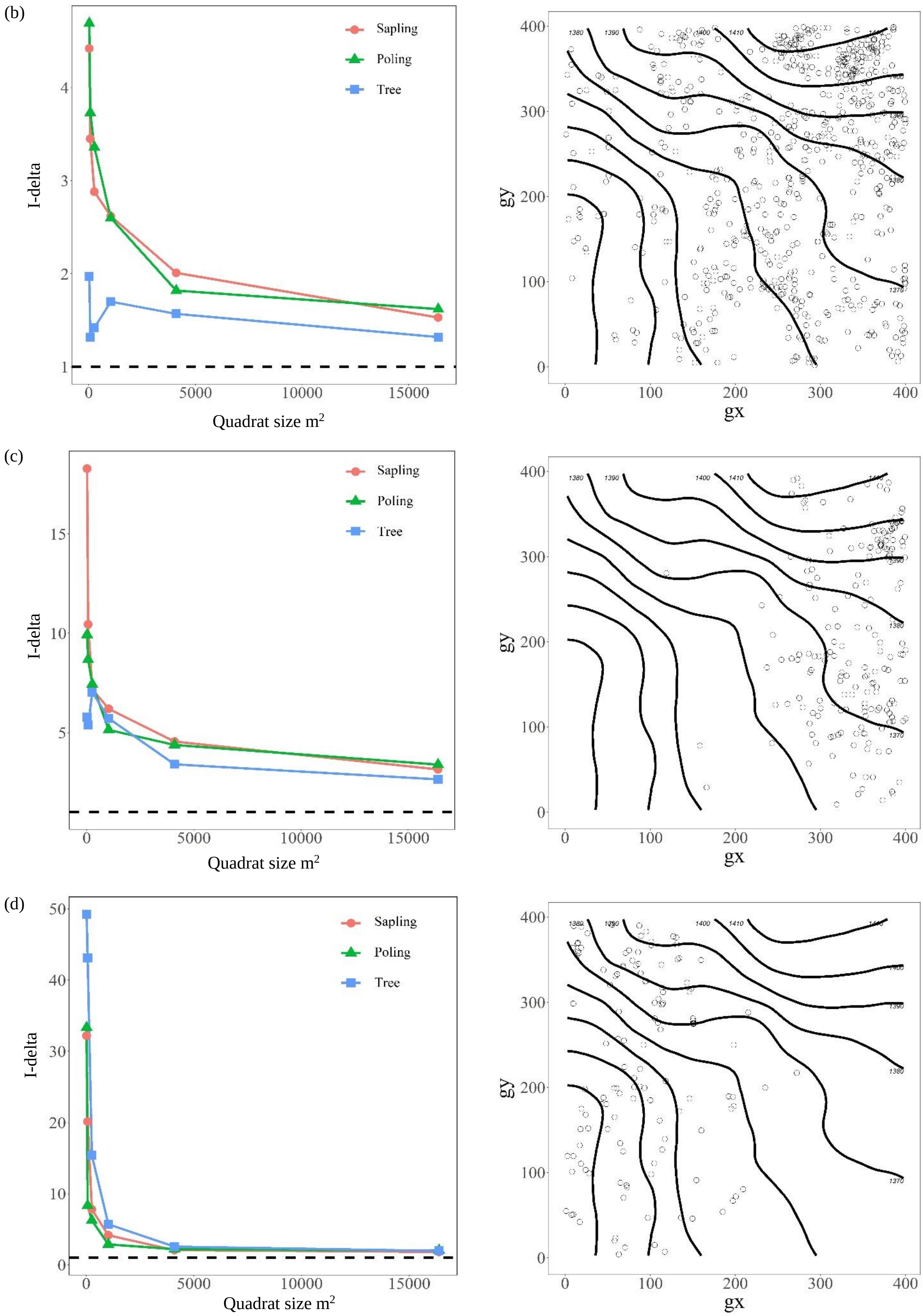


Figure 5. Clumped spatial distribution patterns of dominant Fagaceae at each growth stage in the 16-ha permanent plot at HKM: (a) *Castanopsis accuminatissima*, (b) *C. armata*, (c) *Lithocarpus truncatus*, and (d) *Quercus oidocarpa* (cont.)

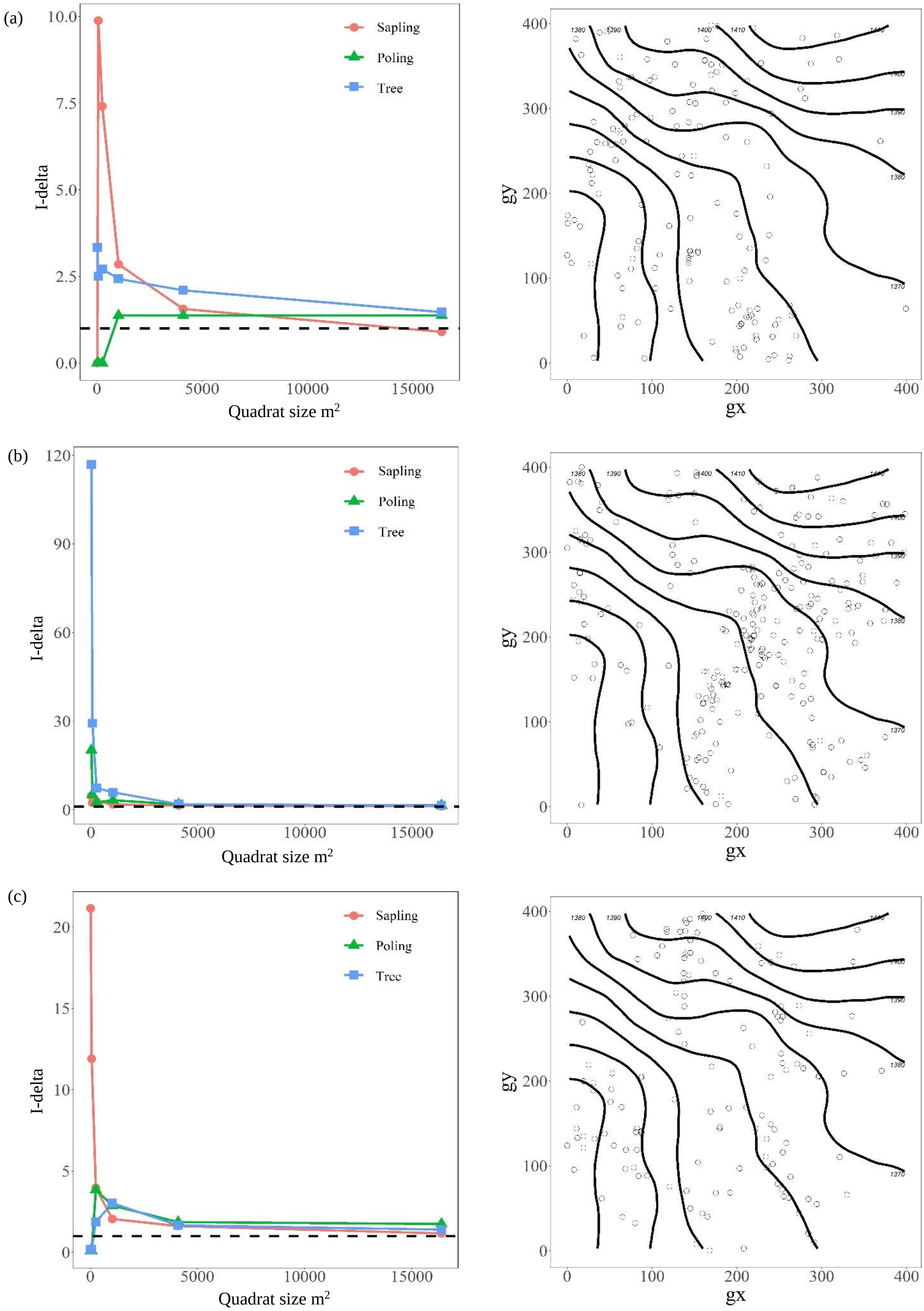


Figure 6. Species with random spatial patterns as saplings and clumped patterns at other stages in the 16-ha plot at HKM: (a) *Mangleitia garetttia*, (b) *Prunus arborea*, (c) *Markhamia stipulata*, and (d) *Bridelia glauca*

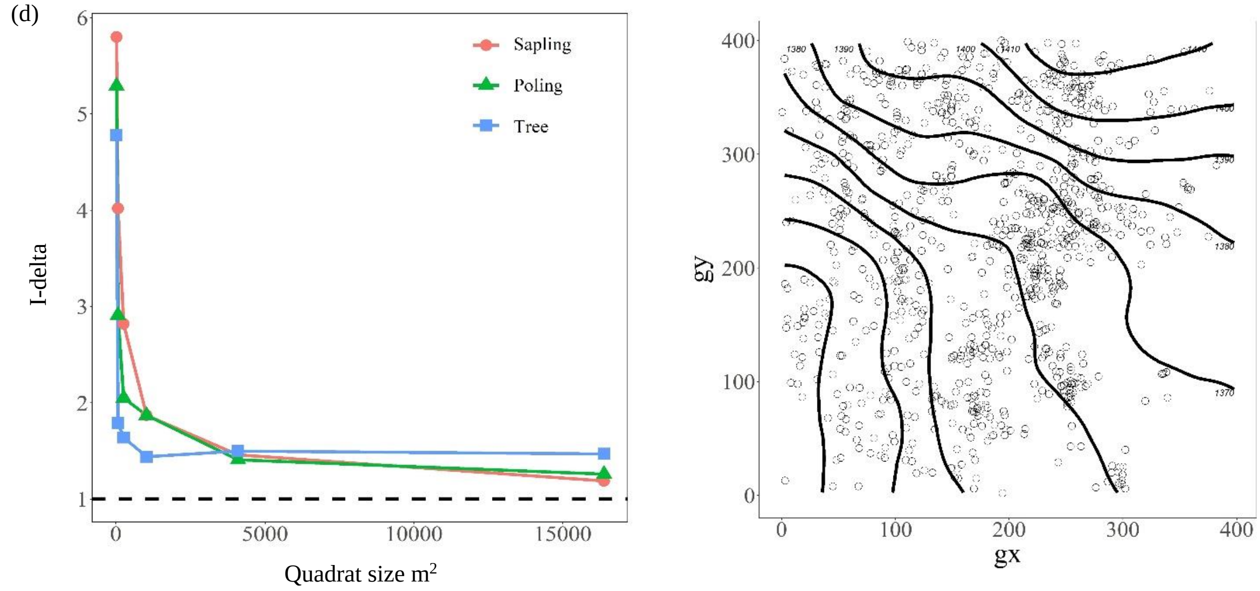


Figure 6. Species with random spatial patterns as saplings and clumped patterns at other stages in the 16-ha plot at HKM: (a) *Mangleitia garetttia*, (b) *Prunus arborea*, (c) *Markhamia stipulata*, and (d) *Bridelia glauca* (cont.)

Clumped spatial patterns are usually observed for tree species in tropical forests. Clumping can be influenced by seed dispersal (Aparajita and Gopal, 2008; Elias et al., 2011). We found that the dominant species of Fagaceae had clumped patterns at every life stage, even though spatial distributions varied among species that preferentially occupied ridge sites (Figure 5). Most species of Fagaceae have acorn or nut fruit types, which fall directly beneath mature trees and generate clumps of saplings around parent trees. Seeds are also eaten by rodents such as squirrels and rats (Rueangket et al., 2019), which are well-known seed predators with strong incisors that enable them to gnaw and consume nuts and other fruits with thick seed coats (Corlett, 2017; Vander Wall, 2001). Some seeds can be distributed by rodents through scatter hoarding. Some seeds may then germinate and become established from forgotten seed caches (Corlett, 2017; Suzuki et al., 2007). By contrast, *Tarenoidea wallichii* (Rubiaceae) has small freshy fruits (Chamchumroon and Puff, 2003; Rueangket et al., 2021), which may facilitate its dispersal by frugivorous birds (Aparajita and Gopal, 2008; Corlett, 2017). Birds not only move seeds away from mature trees, but may also facilitate germination after seeds pass through their digestive system (Murali, 1997). This kind of dispersal typically promotes random rather than clumped patterns, similar to our results.

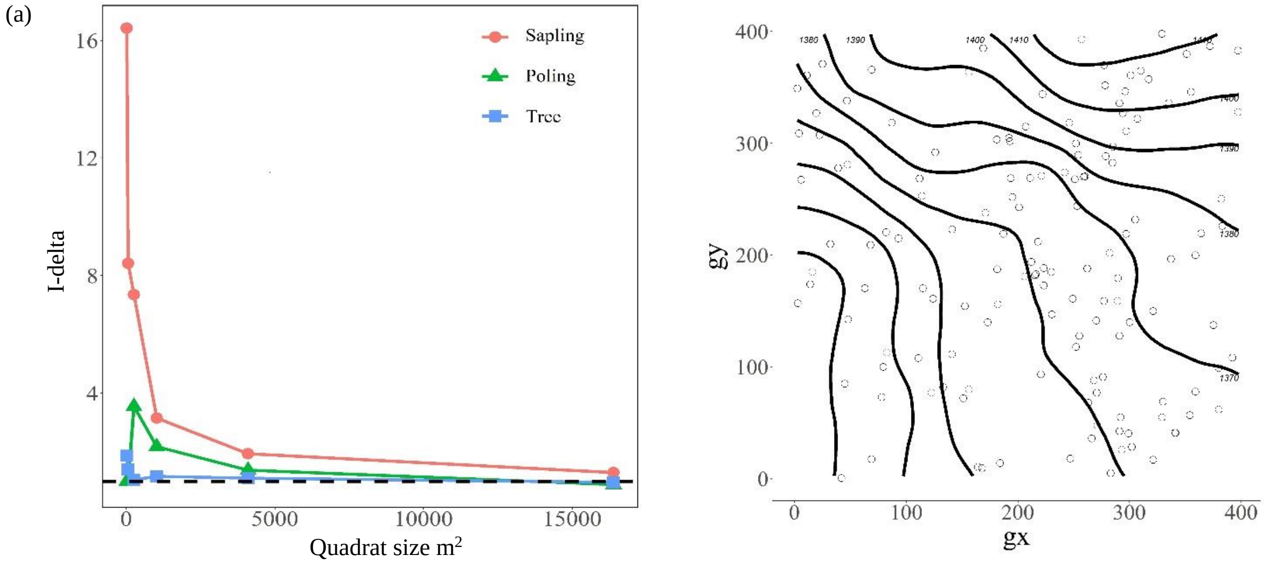


Figure 7. Species with clumped pattern as saplings and random patterns at other life stages in the 16-ha plot at HKM: (a) *Maichelia baillonii*, (b) *Schima wallichii*, and (c) *Canarium euphyllum*, while, and (d) *Tarennoidea wallichii*, which had random spatial patterns at every stage.

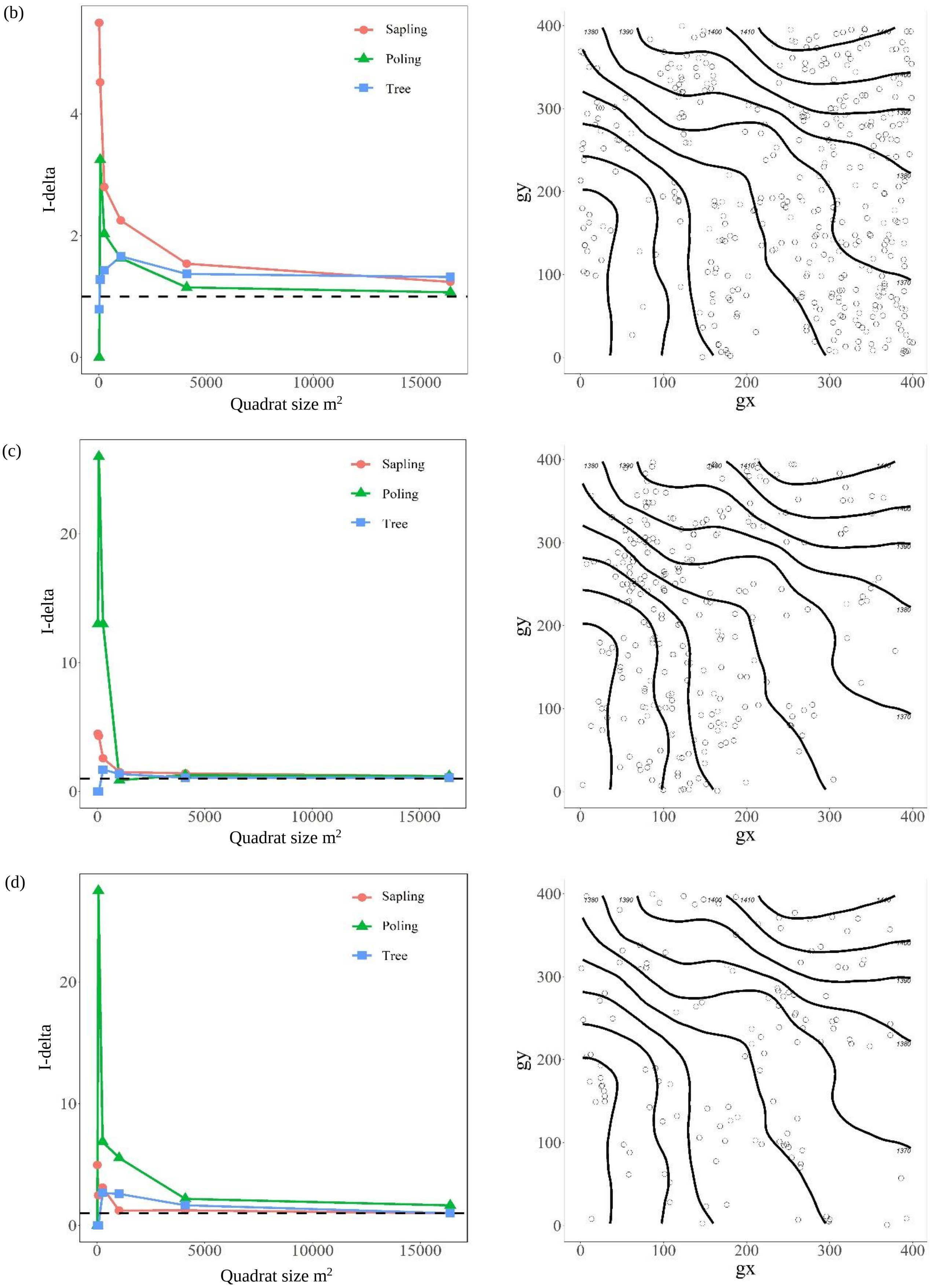


Figure 7. Species with clumped pattern as saplings and random patterns at other life stages in the 16-ha plot at HKM: (a) *Maichelia baillonii*, (b) *Schima wallichii*, and (c) *Canarium euphyllum*, while, and (d) *Tarennoidea wallichii*, which had random spatial patterns at every stage (cont.).

Canarium euphyllum was clumped at the sapling stage but randomly distributed in other stages (Figure 7). Its heavy fruits generally fall close to mature trees (Kitamura et al., 2006), where larger numbers of seedlings and saplings are found than in other places. These dense aggregations of seedlings and saplings experience intense competition and density-dependent mortality, also known as self-thinning (Marod et al., 1999). In this study, survival rates increased with distance from the adult trees, which created a random distribution. Other researchers have reported the effects of natural disturbances on clumped tree species distribution patterns (Bunyavejchewin et al., 2003; Elias et al., 2011; Marod et al., 2021). Environmental changes, particularly the sudden influx of high-intensity light after a big tree falls, can produce clumped tree distributions. Thus, changes in the spatial distributions of trees have implications for all parts of an ecosystem, both biotic and abiotic, and are reflected in different patterns of forest cover and species composition.

4. CONCLUSION

The 16-ha permanent plot in LMF at Doi Suthep-Pui National Park supported high diversity of tree species (220 species in total). The dominant families, based on the numbers of species and population densities, were Fagaceae, Lauraceae, and Theaceae. Tree regeneration based on diameter class distributions suggested that 78 species can maintain their population structure, particularly the dominant species of Fagaceae, *Castanopsis acuminatissima*, *C. tribuloides*, and *Lithocarpus truncata*. Other species had discontinuous unimodal or PO distributions, particularly pioneer species such as *Macaranga indica*, *Morus macroura*, and *Rhus javanica*. These species generally established in canopy gaps, in which the environment was greatly altered and did not support the regeneration of climax species. The establishment of pioneer species may facilitate the development of suitable environments for climax species. Spatial distribution patterns can feed back to affect ecological dynamics, thereby further reinforcing patterns dependent on local interactions. For example, spatial patterns could be affected by the abundance of, and distance to, available resources, as well as by the relationship between seed dispersal and frugivores.

Diameter-class distributions can assist in the evaluation of potential forest sustainability and inform biodiversity conservation plans for species with unimodal or PO distributions. In addition, distributions can inform the selection of species suitable for the LMF restoration program, especially in terms of the appropriate mixtures of pioneer and climax species.

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