BIOTROPIA ISSN: 0215-6334 | e-ISSN: 1907-770X
The Southeast Asian Journal of Tropical Biology
Vol. 31 No. 2, 2024: 291 - 307
DOI: 10.11598/btb.2024.31.2.2023

Review Article

TROPICAL PALMS AND FACTORS INFLUENCING THEIR DISTRIBUTIONS AND DIVERSITY, WITH A FOCUS ON *Pinanga* DIVERSITY IN SOUTHEAST ASIA

Mohamad Farid Abdullah[1], Salwana Md Jaafar[2], Norhayati Ahmad[1,2], Rahayu Sukmaria Sukri[2]

[1]Environmental and Life Sciences Program, Faculty of Science, Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam.
[2]Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam

ARTICLE HIGLIGHTS

- The palm genus *Pinanga* is the most diverse in Southeast Asia.
- Limited ecological studies on *Pinanga* show the influence of environmental factors.
- High *Pinanga* endemism in Borneo requires conservation action.

Article Information

Received: 11 May 2023
Revised: 13 July 2023
Accepted: 14 July 2024

***Corresponding author, e-mail:**
rahayu.sukri@ubd.edu.bn

ABSTRACT

Palms represent some of the keystone species in tropical forests, providing numerous ecosystem services. They are widely studied by botanists because of their iconic and majestic appearance, although ecological studies of palm abundance, distributions, and diversity have only recently begun to gain attention. The abundance and diversity of palms at different spatial scales can be influenced by various factors, such as climate, soil properties, hydrology, topography and forest structure; understanding these influences is essential for conservation. This review details four abiotic factors (climate, soil chemistry, hydrology and topography) and one biotic factor (forest structure) affecting palm distribution and diversity. The genus *Pinanga*, one of the most diverse genera of palms, is discussed in terms of its distribution and diversity in Southeast Asia. Ecological studies on *Pinanga* diversity in the region are examined, revealing the influence of micro- and macro-scale variation in environmental factors, such as litter depth and thickness, canopy openness and crown cover, elevation, slope, aspect, light intensity, humidity and air temperature. The existing knowledge gaps on *Pinanga* ecology in Southeast Asia are discussed, and the need for more studies on population structures, functional traits and determinants of *Pinanga* diversity and distributions within different lowland forest types in the region are highlighted. The high endemism shown by *Pinanga* necessitates a more comprehensive ecological understanding of this genus to better inform its conservation and protection.

Keywords:
borneo, environmental factors, monocots, palmae, plant distributions

INTRODUCTION

Palms (Arecaceae or Palmae) are among the most abundant and important plant life in tropical rainforests (Dransfield *et al.* 2008; Browne & Karubian 2016; Elias *et al.* 2019). They represent one of the oldest surviving monocot families, maintaining their presence in tropical rainforest-like biomes over geological timespans (Renninger & Phillips 2016). Palms occur in tropical and subtropical regions worldwide and are found in a wide range of ecosystem types, including rainforests, montane regions, dry forests, savannas and desert oases (Martins *et al.* 2014; Abdo 2017). In tropical forests, palms are remarkably majestic and can form either dense monodominant palm communities or species-rich communities with many forms of growth (Thonhofer *et al.* 2015; Elias *et al.* 2016; Balslev *et al.* 2016; Mehmud & Roy 2021). Palms display a variety of growth forms, including small shrubs, lianas and large trees (Muscarella *et al.* 2020). It is estimated that 40% of palm species are capable of growing stems of at least 10 cm diameter at 1.3 m above the ground (Kissling *et al.* 2019). Palms can take the form of tall trees entirely by primary growth because they lack secondary growth and vascular cambium (Goodman *et al.* 2013). Some palm trees form thick and shallow root systems that provide better support than those of deep-rooted palm trees (Muscarella *et al.* 2020).

Palms are important to tropical ecosystems because they offer various ecosystem services (Cámara-Leret *et al.* 2017a; Levis *et al.* 2017; Muscarella *et al.* 2020; Montoya *et al.* 2021) and play an important role in forest structure and function (Boukili & Chazdon 2017). Within tropical ecosystems, palms are notable for their high biomass, effects on plant recruitment, interactions with other plants as well as dispersers, and pollinator and nutrient turnover (Montúfar *et al.* 2011; Sørensen 2012). Palms are often considered keystone species in tropical forests due to the dependence of many animals on their flowers and fruits for food (Onstein *et al.* 2017; Macedo-Santana *et al.* 2021). Palms have also functioned as a model system for geographical ecology and rainforest evolution (Kissling *et al.* 2012).

With more than 2,500 recognized species in 183 genera worldwide, palms are one of the most diverse groups of plants (Eiserhardt *et al.* 2011; Baker & Couvreur 2012; Kissling *et al.* 2012; Göldel *et al.* 2015; Baker & Dransfield 2016; Cámara-Leret *et al.* 2017a; Levis *et al.* 2017; Muscarella *et al.* 2020). Palms are common and characteristic elements of tropical forests across the equatorial region (Dransfield *et al.* 2008; Svenning *et al.* 2008; Baker & Couvreur 2013; Reichgelt *et al.* 2018; Bogota-Angel *et al.* 2021). Palm diversity is the highest in tropical Asia, followed by the Americas and Africa (Blach-Overgaard *et al.* 2010; Muscarella *et al.* 2020). Approximately half of all palm species (c. 1,200 species in 57 genera) have been recorded in tropical Asia, most of which are found in Malesia, with almost 1,000 species in 50 genera (Dransfield *et al.* 2008; Renninger & Phillips 2016). Although Malesia is known as the greatest palm diversity hotspot, there is a differentiation in species richness and distribution patterns across the region (Baker & Couvreur 2012). High palm species richness was recorded in both western (302 species in Borneo, 162 species in the Philippines) and eastern Malesia (243 species in New Guinea; Baker & Couvreur 2012). In contrast, lower species richness has been recorded in Wallacea, which comprises Sulawesi, the Moluccas and the Lesser Sunda Islands, with estimates of at least 62, 40 and 6 species, respectively (Baker & Couvreur 2012).

Palm abundance and diversity can have significant effects on tropical forest ecosystem functions as well as carbon sequestration (Muscarella *et al.* 2020). Palms are widely accepted as suitable model organisms for understanding the influence of high tropical biodiversity and geographical variation (Eiserhardt *et al.* 2011; Couvreur & Baker 2013). Therefore, understanding the diversity, distribution and dispersal of palms is integral to their conservation (Dransfield *et al.* 2008; Eiserhardt *et al.* 2011; Bacon *et al.* 2013; Abdo 2017). However, quantitative analyses of the distribution patterns and factors associated with palm abundance and diversity are still lacking (Muscarella *et al.* 2020). Among the palms, the genus *Pinanga* is one of the most diverse (Govaerts *et al.* 2020) and has recently been gaining attention in scientific studies (Mooney 2020; Haji Ramlan 2020; Abdullah 2021). This review focuses on the factors influencing palm abundance and species diversity, as well as the diversity of *Pinanga* palms in Southeast Asia.

FACTORS INFLUENCING PALM ABUNDANCE AND SPECIES DIVERSITY

Global patterns in palm distributions are mainly limited by low temperatures (Moraes *et al.* 2014). An increase in temperature can extend palm distributions to higher elevations where precipitation can then exert a significant positive effect on palm species richness (Renninger & Phillips 2016). Several studies have reported that palm abundance and species richness are strongly correlated with environmental factors (Kahn 1987; Cintra *et al.* 2005; Eiserhardt *et al.* 2011; Kristiansen *et al.* 2011; Manggat 2012; Emilio *et al.* 2014; Scariot 2015; Benchimol *et al.* 2017; Elias *et al.* 2019), and palm species distributions on continental and regional scales are associated with changes in climate, soil properties and dispersal (Blach-Overgaard *et al.* 2010). At smaller scales, palm distributions are associated with topography, hydrology, vegetation structure, species interactions and dispersal, but the relative importance of these factors differs between studies (Vormisto *et al.* 2004; Blach-Overgaard *et al.* 2010; Eiserhardt *et al.* 2011; Sørensen 2012; Alvaro-Segura *et al.* 2012). Here, we review four abiotic factors (climate, soil chemistry, hydrology and topography) and one biotic factor (forest structure) that influence palm abundance and species diversity (Eiserhardt *et al.* 2011).

Climate

Palm species distribution studies have primarily focused on the role of the environment, with climate often regarded as the main range-limiting factor, especially at large spatial scales (Blach-Overgaard *et al.* 2010). Climate plays a crucial role in global palm distribution (Muscarella *et al.* 2020; Bogota-Angel *et al.* 2021), and the distribution of individual palm species and patterns of palm species richness and diversity across different vegetation types are strongly associated with climate (Svenning *et al.* 2008; Eiserhardt *et al.* 2011; Sevegnani *et al.* 2016). Previous studies also observed that climate is important in determining plant distribution and diversity (Pearson & Dawson 2003; Kreft & Jetz 2007). Palm diversity hotspots, such as the Sunda region, offer beneficial conditions for diversification in palms due to the prolonged periods of climatic stability, while poor palm diversity can be observed in the Lesser Sunda Islands due to their moderately dry, seasonal climate (Baker & Couvreur 2012).

Palm diversity is strongly correlated with climatic factors, especially water (Bjorholm *et al.* 2005), with precipitation having the strongest positive effect on palm species richness (Renniger & Philips 2016). Similarly, climate has the greatest influence on the distributions of palms, which appear to be more significantly influenced by water-related variables than by temperature (Blach-Overgaard *et al.* 2010; Sørensen 2012). Additionally, palm species richness is influenced by annual precipitation or the number of wet days (Sørensen 2012). This supports a broad-scale study of species richness conducted by Hawkins *et al.* (2003), who concluded that water-related factors, such as rainfall and precipitation, are excellent drivers of plant richness in tropical and subtropical areas. Blach-Overgaard *et al.* (2010) concluded that climate was more important than habitat and human impact in determining the distribution of 25 out of 29 African palm species, with most of the palm species studied preferring humid climates, and few being influenced by temperature. In addition, palm species distributions within subtropical and temperate regions are often restricted due to low temperatures (Gatti *et al.* 2008). Therefore, palms are most diverse in warm and humid regions (Eiserhardt *et al.* 2011).

Studies focusing on the influence of climatic variables on palm species richness and diversity are limited (Dransfield *et al.* 2008), with the influence of climatic factors on palm species distributions within tropical regions evaluated for African palms only (Blach-Overgaard *et al.* 2010). Temperature seasonality has been observed to limit palm distributions and emphasizes climate as the main range determinant at large spatial scales (Pearson & Dawson 2003). However, it is increasingly understood that palm species distributions are sensitive to climate at multiple spatial scales (Blach-Overgaard *et al.* 2010), and therefore, more studies at both local and global scales are recommended (Eiserhardt *et al.* 2011).

Soil Properties

Most tropical plant species show strong associations with edaphic conditions, and soil fertility can influence tree community composition (John *et al.* 2007; Sukri *et al.* 2012). Palms also show habitat associations governed by soil properties (Vormisto *et al.* 2004; Andersen *et al.* 2010; Viana *et al.* 2021). Soil fertility is the second most important abiotic factor influencing palm species richness (Bjorholm *et al.* 2006). For example, the diversity of palm subfamilies Arecoideae and Calamoideae tends to increase with increasing soil fertility (Bjorholm *et al.* 2006). Similarly, the link between soil properties and palm community composition in lowland rainforests is well studied (Vormisto *et al.* 2004; Andersen *et al.* 2010), and palm community compositions are linked with soil properties, such as exchangeable base concentration, aluminum concentration and soil texture (Cámara-Leret *et al.* 2017b).

Studies have shown that soil chemistry can affect palms species' abundance and richness (Ruokolainen & Vormisto 2000; Svenning 2001; Bjorholm *et al.* 2006; Poulsen *et al.* 2006; Eiserhardt *et al.* 2011; Muscarella *et al.* 2020). The distribution and abundance of several tropical American palm species are correlated with soil factors, such as nutrient concentrations, aluminum content and clay (Svenning 2001). Palm species in the western Amazon prefer either nutrient-poor or nutrient-rich soils (Ruokolainen & Vormisto 2000), and the composition of Amazon palm communities is significantly correlated with soil chemical properties, such as exchangeable cations and aluminum content (Poulsen *et al.* 2006; Dalling *et al.* 2016; Viana *et al.* 2021). Macronutrients, such as exchangeable bases (calcium, potassium and magnesium) and phosphorus, were found to influence species abundances in palm communities in non-flooded Amazonian forests more significantly than micronutrients did (Cámara *et al.* 2017b). Similarly, exchangeable bases, phosphorus and nitrogen concentrations have been linked to the distribution of palms in various lowland tropical rainforests (Andersen *et al.* 2010; Baribault *et al.* 2012; Condit *et al.* 2013). Soil bulk density can also influence the composition of palm communities (Andersen *et al.* 2010; Viana *et al.* 2021), and palms can show variation across gradients of soil nutrient availability (Viana *et al.* 2021). Palm species composition can also vary with soil texture on local scales, likely due to a soil texture correlation with drainage (Kristiansen *et al.* 2012; Sørensen 2012).

In contrast, some studies have also found that differences in soil properties may not be important in influencing individual palm species' distributions at continental scales, and not all studies support a significant role for soil fertility in palm community turnover (Normand *et al.* 2006; Blach-Overgaard *et al.* 2010). Therefore, the strength of soil effects on palm community composition is variable and may depend on the spatial scale, ecosystem and habitat (Eiserhardt *et al.* 2011; Viana *et al.* 2021). Moreover, soil chemistry often interrelates with other environmental factors, such as topography, hydrology and vegetation structure, which requires further study (Eiserhardt *et al.* 2011).

Hydrology

Plant species distributions and diversity are also affected by hydrology, particularly through flooding and drainage (Eiserhardt *et al.* 2011). As precipitation is one of the most important predictors of palm species richness (Kissling *et al.* 2012), this correlates with a higher abundance of palms in continually wet sites (Viana *et al.* 2021). The importance of hydrology for palm species distribution has been well demonstrated for Amazonian palms (Kahn 1987). Several studies have assessed the effects of flooding and drainage on the distribution and abundance of individual palm species (Svenning 2001; Montúfar & Pintaud 2006). Most palms are linked with either well-drained or poorly-drained soils (Henderson *et al.* 2019), while some palm species prefer swampy areas (Dransfield *et al.* 2008). For instance, most of the African palms occupy humid rainforests or swamplands, and are often in the riparian zone or areas where the water table is locally high, while very few species are found in dry and open habitats, such as savannas or deserts (Blach-Overgaard *et al.* 2010). Palm species abundance in French Guiana is correlated with a change in soil drainage along topographic transitions (Salm *et al.* 2015). Additionally, Salm *et al.* (2015) found that the abundance of the six most common palm species was correlated with humidity gradients from floodplains to terra firme, with palm distribution from the most flood-tolerant to the least flood-tolerant palm species.

Differences in soil moisture and drainage have been shown to affect palms individually (Svenning 2001). For example, five out of 23 palms responded individually to poor drainage in the Amazonian terra firme forest (Svenning 1999). Significant differences in palm community composition between well-drained and poorly-drained soils have been recorded (Balslev *et al.* 1987; Kahn 1987; Normand *et al.* 2006). For instance, palms in the terra firme (dry land) consisted of 17% of individuals and 11% of the basal area, compared with 30% of individuals and 19% of the basal area in the floodplain forest in Ecuador (Balslev *et al.* 1987). Palm species richness in seasonally flooded land and terra firme forests in the Amazon basin was found to be three times higher on well-drained soils (terra firme) than on seasonally flooded soils (Kahn & de Castro 1985). Similarly, in the western Amazon, higher species richness was recorded for palm communities in terra firme forests than in wetland forests (Eiserhardt *et al.* 2011), and in Ecuador, palm species were found to be significantly more abundant in terra firme forests than in floodplain forests (Balslev *et al.* 1987). Although flooding and drainage have strong effects on palm distribution on local to landscape scales, as well as on palm species richness on a landscape scale (Eiserhardt *et al.* 2011), the degree to which these effects are influenced by other factors, such as vegetation structure and light availability, requires further investigation (Svenning 2000).

Topography

Topography strongly affects the distribution of tropical plant species (Sukri *et al.* 2012; Wang *et al.* 2015; Limin *et al.* 2022) and is known as a key influencing factor for vegetation patterns at the landscape and regional scales (Sanders & Rahbek 2012; Moeslund *et al.* 2013). Plant species diversity is often related to topographic heterogeneity at broader scales (Kreft & Jetz 2007). Topography indirectly affects plant distributions by regulating other abiotic factors, such as soil conditions, wind exposure, hydrology, temperature, climate and forest structure (Svenning 2001; Balslev *et al.* 2011; Eiserhardt *et al.* 2011; Lueder 2020).

Palm species abundance, richness and composition have a significant relationship with altitude (Rodrigues *et al.* 2014). Palms decrease in abundance with increasing soil moisture and decreasing elevation, indicating that elevation and soil moisture influence palm community patterns (Bonetti *et al.* 2017; Lueder 2020). Kreft *et al.* (2006) found that rare palm species were more strongly influenced by topographic complexity, while climatic factors were strongly correlated with species richness for widespread species. At landscape scales, topography shows a correlation with palm abundance (Eiserhardt *et al.* 2011). For instance, the abundance of canopy palms in Costa Rica and wet Amazonian forests was the highest on crests and steep slopes than at lower altitudes (Kahn 1987). In a seasonally dry forest in southern Amazonia, palm abundance decreased with elevation (Salm *et al.* 2007), while in Costa Rica, palms are abundant at lower elevations (approx. 2,500 m altitude; Lieberman *et al.* 1996). Eiserhardt *et al.* (2011) suggested that high palm abundance in steep and rugged terrain was due to a high number of canopy gaps that were favorable for palm recruitment, while the lower abundance of palms on steep slopes compared with crests may be due to the high water overflow causing those sites to be extremely dry for palms (Kahn 1987). Additionally, Salm *et al.* (2007) showed that the high abundance of palms in low-lying areas was due to high moisture availability. At a local scale, palm species abundance differed independently of topographic position in both Amazonian lowland rainforests and seasonally dry forests (Kahn 1987; Salm *et al.* 2007). In Amazonian Ecuador, 10 out of 23 palm species were related to specific topographic positions, while altitude and inclination tended to be less important; the opposite pattern was seen in the wet lower montane forest in Ecuador, where altitude and aspect strongly influence palm species distributions (Svenning 1999, 2001).

In terms of species richness, both palm species richness and genus richness decrease significantly with elevation in New Guinea and its adjacent islands (Bachman *et al.* 2004). However, topography may be less influential on palm species richness at a continental scale in the Americas (Bjorholm *et al.* 2005; Kreft *et al.* 2006). On a landscape scale, palm species richness tends to decline with elevation in the Amazon rainforest (Salm *et al.* 2007) and along an altitudinal transect in Costa Rica (Lieberman *et al.* 1996). In contrast, Poulsen *et al.* (2006) found that the species richness of palms was the highest at the highest elevations in terra firme Amazonian rainforest. Overall, topography is important at local scales but may be less important in influencing palm species richness at broader spatial scales (Bjorholm *et al.* 2005; Kristiansen *et al.* 2011). Topography only influences palm species distributions and community composition indirectly; thus, its effects will vary for local scale differences depending on the geographical features of each location (Vormisto *et al.* 2004). It is also suggested that the relationship between diversity and elevation depends fundamentally on the interaction of environmental variables (Rahardjo 2020). Consequently, it is important to measure other environmental factors, such as soil water availability, soil nutrient conditions, hydrology, wind exposure and light availability, which are factors that directly underlie topographic gradients (Svenning 2001; Eiserhardt *et al.* 2011), and to determine how topographic variables can influence the population dynamics of palms (Pasion *et al.* 2022).

Forest Structure

Forest structure reflects the role of plants and specific trees as ecosystem engineers that can influence environmental factors, such as light availability and litter fall (Svenning 2001). The surrounding vegetation and canopy gaps can influence microclimate and light availability (Carson & Schnitzer 2011), and light influences species distribution through competition for light and through shade tolerances (Carson & Schnitzer 2011). In palm communities, several palm species favor an open canopy due to light availability (Eiserhardt *et al.* 2011). For example, rattan occurrence is positively correlated with the presence of treefall gaps (Siebert 2005). In addition, Svenning (2000) found that several palms prefer gaps and are distributed non-randomly with canopy openness. The importance of light on palms may differ between ontogenetic stages (Svenning 2001). Previous studies have suggested that large palms can reach the adult stage only in treefall gaps due to their light requirements increasing at the adult stage (Eiserhardt *et al.* 2011)

There are no strong relationships between canopy heterogeneity or light availability and palm community composition (Eiserhardt *et al.* 2011). For example, canopy openness and the presence of non-palm trees in Amazonian terra firme rainforest does not significantly influence palm species richness (Cintra *et al.* 2005).

However, the community composition of palms is associated with forest structure (Browne & Karubian 2016), where adult palm abundance and species richness tend to increase with canopy height, while juvenile abundance decreases with canopy openness. Juvenile species richness was also found to increase with distance to the forest edge and decrease with canopy openness (Browne & Karubian 2016). Hilário and Toledo (2016) observed that forests with taller and larger trees, a closed canopy and an open understory contain higher palm abundance. However, Eiserhardt *et al.* (2011) argued that the influence of vegetation structure on the species richness of palms may be weak, as only a few palm species respond to canopy openness or light availability, likely due to species-specific preferences.

GENUS Pinanga

The genus *Pinanga* Blume (1838) is a genus of palms in the family Arecaceae (Syauqina *et al.* 2017; Randi *et al.* 2019) and is one of the most diverse genera of palms (Govaerts *et al.* 2020). Arecaceae are persistent climbers, bushes and trees (Mainasara *et al.* 2019). The growth forms of *Pinanga* are varied, including shrubs and tree-like or stemless plants (Dransfield *et al.* 2008). The genus shows significant differences in morphological and quantitative characteristics, such as size, form, stem color, crown shaft, leaves and pollen (Randi *et al.* 2019). *Pinanga* palms can be distinguished from other palms by the entire margins of the blades of their leaves or leaflets, and by their inflorescences, flower arrangements and fruits (Ang *et al.* 2010). *Pinanga* can be found in a variety of habitats because each species typically prefers different environments (Dransfield 1980; Fernando *et al.* 2020). For example, *Pinanga simplicifrons* (Miq.) Becc. is found in shaded and swampy areas (Ang *et al.* 2010), while *Pinanga javana* Blume prefers hill slopes (Zulkarnaen *et al.* 2019). Some *Pinanga* species prefer higher elevations (Syahida-Emiza *et al.* 2018; Fernando *et al.* 2020).

Local communities often use *Pinanga* palms as tools and sources of food. For example, the stalk of *Pinanga auriculata* Becc. is used to make fish traps, while edible fruit from *Pinanga patula* Blume var. *microcarpa* Becc. can be eaten with betel (Haji Ramlan 2020). In Bali (Indonesia), *Pinanga arinasae* Witono (locally known as Nyabah or Jabah) leaves, fruits as well as stems are culturally important for Balinese people (Sutomo *et al.* 2018). Local people mostly use *P. arinasae* for ornamental purposes (Syauqina *et al.* 2017; Sutomo *et al.* 2018), such as the production of traditional umbrellas called 'Cukup' from the *P. arinasae* leaf sheath (Sutomo *et al.* 2018). The extract from *Pinanga limosa* Ridl. may function as a potential anticancer agent, although its efficacy requires verification (Mainasara *et al.* 2019).

Distribution of *Pinanga* Species

Currently, a total of 145 species of *Pinanga* have been recorded worldwide (POWO 2024) and their distributions range from the Himalayas and South China to New Guinea, with high diversity at the Sunda Shelf, while they are poorly represented in Papuasia (Coode *et al.* 1996; Randi *et al.* 2019). Within Southeast Asian tropical rainforests, *Pinanga* typically displays prominent levels of endemism and high species diversity (Dransfield *et al.* 2008). The Southeast Asian region is the center of *Pinanga* diversity worldwide, with 140 species of *Pinanga* recorded (Govaerts *et al.* 2020; Zulkarnaen *et al.* 2022a). The highest *Pinanga* species richness has been recorded in Malaysia and Indonesia (61 and 49 species, respectively), while Cambodia and Laos are the least species-rich countries (1 species each; Fig. 1). No records of *Pinanga* species have been published to date for Timor-Leste. These differences in species richness of *Pinanga* in the Southeast Asian countries partly reflect the larger amounts of sampling effort and studies that have been conducted in Malaysia and Indonesia compared to countries, such as Cambodia, Laos and Timor-Leste.

As studies on palm communities have gained increasing attention in the past ten years, *Pinanga* palms have been discovered in various locations in Southeast Asia during this period (Ang *et al.* 2010; Loo *et al.* 2014; Syauqina *et al.* 2017; Randi *et al.* 2019; Fernando *et al.* 2020; Lim *et al.* 2022). In Singapore, Ang *et al.* (2010) rediscovered *P. simplicifrons*, which was widely regarded as nationally extinct in Singapore before this rediscovery. *P. simplicifrons* was also rediscovered near Lornie Trail at the edge of MacRitchie Reservoir, Singapore (Lim *et al.* 2022). These rediscoveries in specific localities have led to the assessment of *P. simplicifrons* as 'critically endangered' in Singapore (Ang *et al.* 2010; Loo *et al.* 2014; Lim *et al.* 2022), although it remains unassessed in the IUCN Red List (IUCN 2024). In Malaysia, the *Pinanga* genus was the third most dominant palm genera recorded in the Dered

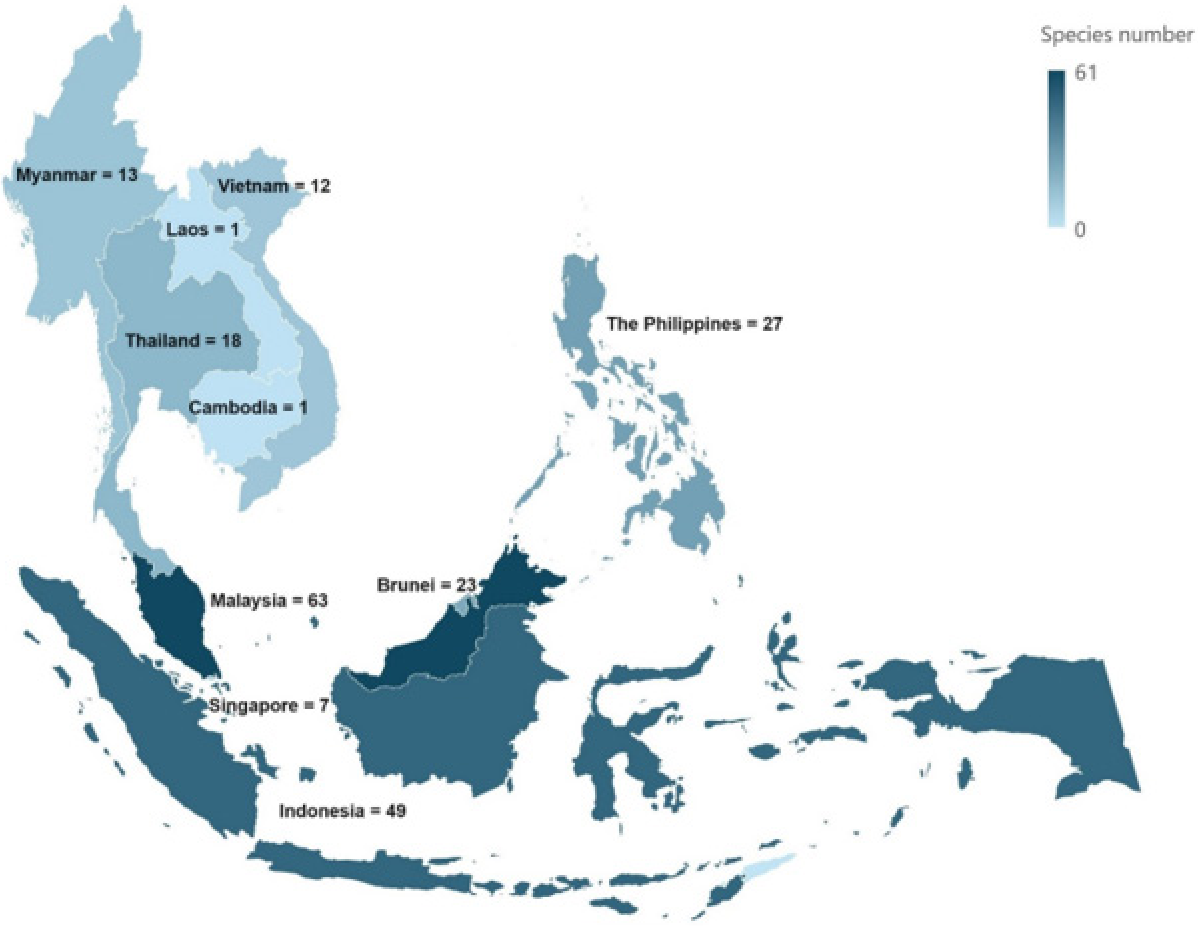

Figure 1 Variation in species richness of *Pinanga* across Southeast Asia

Notes: The total number of *Pinanga* species recorded in each country was compiled from Coode *et al.* (1996), Ang *et al.* (2010) and POWO (2024).

Krian National Park after the genera *Calamus* and *Daemonorops*, while *Pinanga chaiana* J.Dransf., *Pinanga crassipes* Becc. and *Pinanga jambusana* C.K.Lim were found scattered along trails in this national park (Syauqina *et al.* 2017). During an expedition to Long Banga, Sarawak, at least 11 palm species were found at higher ridges, including an unidentified species of *Pinanga* (Syahida-Emiza *et al.* 2018). In Indonesia, *P. arinasae* was found in the Pilan Forest in Bali (Wahyuni *et al.* 2017), although the species was previously suggested to be present only in Mt. Tapak Bedugul, Bali (Witono *et al.* 2002; Sutomo *et al.* 2018). *Pinanga schwanerensis* Randi, Hikmat & Heatubun was newly discovered in Kalimantan, growing on undulating grounds and steep slopes (Randi *et al.* 2019). *Pinanga lepidota* Rendle was rediscovered on Palawan Island in 2020, increasing the number of *Pinanga* species recorded in the Philippines to 27 (Fernando *et al.* 2020). In Vietnam, *Pinanga spiralis* A.J.Hend. & N.Q.Dung was discovered by Henderson and Dung (2017).

Within Borneo, a total of 41 species of *Pinanga* have been recorded (Table 1), mostly from Sarawak, Brunei Darussalam and Sabah (Odufuwa 2019; Govaerts *et al.* 2020; POWO 2024). Fewer records of *Pinanga* have been found in Kalimantan, Indonesian Borneo, despite the larger land area and greater habitat diversity (Randi *et al.* 2019; Odufuwa 2019). The higher species richness in Malaysian Borneo likely partly reflects greater sampling efforts compared to Kalimantan. Notably, despite having the smallest land area within Borneo, 23 species of *Pinanga* have been recorded in Brunei Darussalam. Almost all of the *Pinanga* species recorded in Borneo are endemic to the island (POWO 2024), with the exception of three species (*P. auriculata*, *P. patula* and *P. simplicifrons*).

Table 1 Checklist of *Pinanga* species recorded in Borneo

No.	Species	Brunei	Sabah	Sarawak	Kalimantan
1	*Pinanga albescens* Becc.		X	X	X
2	*Pinanga angustisecta* Becc.	X	X	X	
3	*Pinanga aristata* (Burret) J.Dransf.	X	X	X	X
4	*Pinanga arundinacea* Ridl.		X	X	
5	***Pinanga auriculata* Becc.**	X	X	X	
6	*Pinanga borneensis* Scheff.	X	X	X	X
7	*Pinanga brevipes* Becc.	X	X	X	X
8	*Pinanga capitata* Becc.	X	X	X	X
9	*Pinanga chaiana* J.Dransf.	X	X	X	
10	*Pinanga crassipes* Becc.		X	X	
11	*Pinanga cucullata* J.Dransf.			X	
12	*Pinanga decora* L.Linden & Rodigas		X	X	
13	*Pinanga dumetosa* J.Dransf.	X	X	X	
14	*Pinanga gracillima* Merr.		X	X	
15	*Pinanga jambusana* C.K.Lim			X	
16	*Pinanga keahii* Furtado		X	X	X
17	*Pinanga lepidota* Rendle	X	X	X	X
18	*Pinanga ligulata* Becc.		X	X	X
19	*Pinanga limbangensis* C.K.Lim			X	
20	*Pinanga minuta* Furtado.	X	X	X	
21	*Pinanga mirabilis* Becc.	X	X	X	X
22	*Pinanga mooreana* J.Dransf.	X		X	
23	*Pinanga pachyphylla* J.Dransf.			X	
24	***Pinanga patula* Blume**	X	X	X	X
25	*Pinanga pilosa* (Burret) J.Dransf.		X	X	
26	*Pinanga ridleyana* Becc.	X	X	X	X
27	*Pinanga rivularis* Becc.	X		X	
28	*Pinanga rupestris* J.Dransf.			X	
29	*Pinanga salicifolia* Blume	X	X	X	X
30	*Pinanga schwanerensis* Randi, Hikmat & Heatubun				X
31	*Pinanga sessilifolia* Furtado	X	X	X	X
32	***Pinanga simplicifrons* (Miq.) Becc.**	X	X	X	X
33	*Pinanga stricta* Becc.		X	X	
34	*Pinanga subterranea* Randi & W.J.Baker			X	X
35	*Pinanga tenacinervis* J.Dransf.			X	
36	*Pinanga tenella* (H.Wendl.) Scheff.	X	X	X	X
37	*Pinanga tomentella* Becc.	X	X	X	X
38	*Pinanga trichoneura* Becc.		X	X	
39	*Pinanga variegata* Becc.	X	X	X	X
40	*Pinanga veitchii* H.Wendl. ex H.J.Veitch	X		X	
41	*Pinanga yassinii* J.Dransf.	X			
	Total number of species	**23**	**29**	**39**	**19**

Notes: Presence of each palm species in a country or state in Borneo was indicated by an 'X'. All species are Bornean endemics, with the exception of three species highlighted in bold.

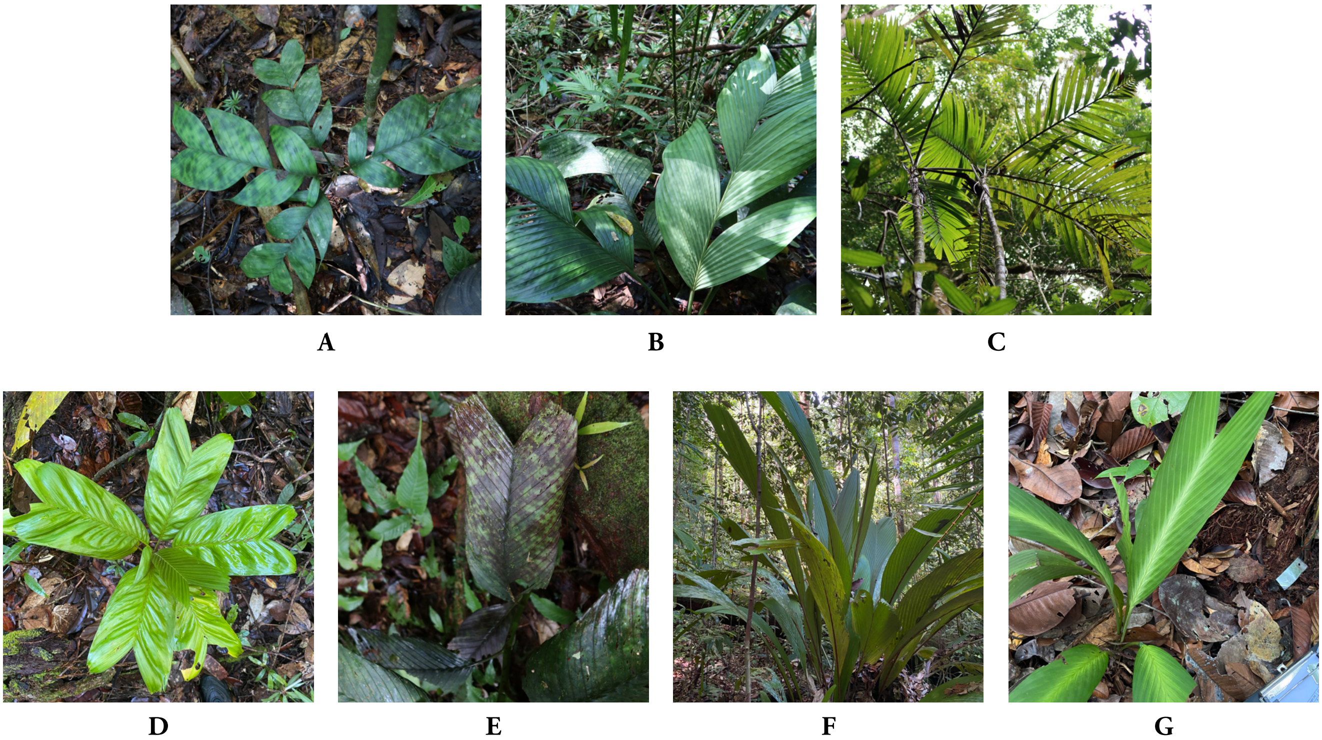

Figure 2 Selected *Pinanga* species found in Brunei Darussalam: A. *Pinanga aristata* (Burret) J.Dransf.; B. *Pinanga* aff. *brevipes* Becc.; C. *Pinanga mooreana* J.Dransf.; D. *Pinanga lepidota* Rendle; E. *Pinanga veitchii* H.Wendl. ex H.J.Veitch; F. *Pinanga mirabilis* Becc. and G. *Pinanga chaiana* J.Dransf.

Ecological Studies on *Pinanga* in Southeast Asia

In Southeast Asia, most published studies on *Pinanga* palms have focused on checklists and descriptive notes on the *Pinanga* species found within a country (Ang *et al.* 2010; Henderson *et al.* 2010; Adorador *et al.* 2020; Fernando *et al.* 2020). Despite increased attention on documenting *Pinanga* diversity within Southeast Asia, studies focusing on *Pinanga* ecology remain limited. Similarly to other palms, *Pinanga* distributions are often shaped by both micro- and macro-scale variation in environment. Within Southeast Asia, studies have shown the influence of a variety of environmental factors, such as litter depth and thickness, canopy openness and crown cover, elevation, slope, aspect, light intensity, humidity and air temperature (Syauqina *et al.* 2017; Astuti *et al.* 2018; Randi *et al.* 2019; Zulkarnaen *et al.* 2019, 2022a,b; Iryadi & Sutomo 2020; Yudaputra *et al.* 2021).

A study by Yudaputra *et al.* (2021) investigating the ecology of endemic *P. arinasae* in Bali showed that litter depth, canopy openness, elevation, slope and aspect were the most important environmental factors influencing this species' occurrence. In addition, microclimatic conditions, such as light intensity, humidity and air temperature, were recorded as significant influencing factors, with light intensity considered the main factor influencing the distribution and abundance of *P. arinasae* (Iryadi & Sutomo 2020). Similarly, the population structure and habitat preferences of *P. javana* at Mt. Slamet (Central Java, Indonesia) were investigated (Zulkarnaen *et al.* 2019). The study showed that the population of *P. javana* was dominated by adult palms on the southern slope of Mt. Slamet and that slope, litter thickness and crown cover influenced the species' density. *Pinanga* palms are also frequently found in humid areas covered by high canopy cover, near small rivers and in soil with thick litter layers, as well as in limestone areas (Syauqina *et al.* 2017; Randi *et al.* 2019). Another study by Zulkarnaen *et al.* (2022b) found that Mt. Slamet was dominated by *P. javana* and *Pinanga coronata* Blume, with *P. javana* found above waterfall areas or on hill slopes. The growth of *P. javana* in Mt. Slamet appears to require specific abiotic factors, such as slope, litter thickness and canopy cover (Astuti *et al.* 2018). In contrast, *P. coronata* individuals were recorded under the heavy shade of the canopy (Zulkarnaen *et al.* 2022a). In Mt. Ungaran (Central Java), *P. javana* was found to be strongly correlated with a stable and humid microclimate, similarly to the *P. javana* found in Mt. Slamet (Zulkarnaen *et al.* 2019, 2022b). This suggests that humidity levels can significantly influence *P. javana* populations. Furthermore, *P. javana* seems to prefer locations with steep to very steep slopes (Zulkarnaen *et al.* 2022a). In Kalimantan, Randi *et al.* (2019) found that *P. schwanerensis* grows on uneven terrain and slopes between 150-550 masl (meters above sea level), and prefers a humid area, high forest cover and thick leaf litter, as well as locations near streams. Other studies, such as those in the Philippines, Vietnam and Singapore, provide little information on the ecology of *Pinanga* palms, typically only including information on their altitude occurrences and locality (Ang *et al.* 2010; Henderson & Dung 2017; Fernando *et al.* 2020; Lim *et al.* 2022). For instance, on Palawan Island, *P. lepidota* is found in Dipterocarp forest at an elevation of 600 m, while *P. lepidota* in Borneo can be found up to an elevation of 1,500 m (Fernando *et al.* 2020). *P. spiralis* in Vietnam is found in lowland rainforests at elevations between 200-550 m (Henderson & Dung 2017). *P. simplicifrons* favors an open area caused by tree falls, and under high canopy cover (Lim *et al.* 2022), and can also survive in swampy areas with rich alluvial soil (Ang *et al.* 2010).

In Brunei Darussalam, a total of 23 species of *Pinanga* have been recorded (Fig. 2), and most of these were recorded in Ulu Temburong National Park (Coode *et al.* 1996; Haji Ramlan 2020). These *Pinanga* species are found in different habitats, from gentle to steep slopes, sandy to clay soil, and at various altitudes; additionally, most of the species are shrubs and are found near running streams (Coode *et al.* 1996). This indicates that *Pinanga* may have specific preferences for soil and environmental conditions.

Several recent studies have focused on the ecology of *Pinanga* palms in Brunei Darussalam. The distributions of *Pinanga* species in Brunei Darussalam are shaped by many factors, such as topographic positions, vegetation structure and soil properties. Shapcott *et al.* (2022) investigated the populations of five co-occurring *Pinanga* species at Kuala Belalong, Ulu Temburong, and found that the population sizes of most of these species were maintained 20 years later, with two species (*P. brevipes* and *P. aristata*) declining in overall abundance. They attributed the decline of understory *Pinanga* palms to the possible influence of climate change due to increased rainfall fluctuations at Kuala Belalong (Shapcott *et al.* 2022). Also at Kuala Belalong, Mooney (2020) investigated the landscape distribution of *Pinanga* and concluded that one group of species (*P. mooreana* and *P. minuta*) was strongly associated with ridges, while a second group (*P. aristata*, *P. brevipes*, *P. dumetosa* and *P. veitchii*) was more strongly associated with valleys. The complex topography of the Kuala Belalong area (Sukri *et al.* 2012) appears to have created a range of microhabitats that enabled *Pinanga* species to coexist within the landscape. At two contrasting mixed Dipterocarp forest sites in Brunei Darussalam (Belalong and Teraja), Haji Ramlan (2020) recorded the influence of soil properties on *Pinanga* species richness, with higher *Pinanga* species richness recorded in Belalong due to higher concentrations of soil nutrients (total P, Mg, Ca, total and exchangeable K) and higher soil organic matter content, soil pH and soil gravimetric water content at this site. Abdullah (2024) recorded distinct *Pinanga* community composition between heath and mixed Dipterocarp forest types in Brunei Darussalam, with five *Pinanga* species (*P. aristata*, *P. chaiana*, *P. mooreana*, *P. variegata* var. *hallieriana* and *P. veitchii*) more strongly linked with the mixed Dipterocarp forest sites and two *Pinanga* species (*P. lepidota* and *P. salicifolia*) more strongly linked with the heath forest sites. Focusing specifically on the foliar nutrient content of *Pinanga* species, Abdullah (2021) examined its variation in three *Pinanga* species (*P. lepidota*, *P. mooreana* and *P. mirabilis*) with contrasting habitats and leaf formations. The study found that those foliar nutrient concentrations differed between the three *Pinanga* species and differed between different leaf formations of the same species. However, further investigations are required to relate the relationship between foliar nutrient concentrations and soil variables to further examine the ecology and habitat adaptations of these three *Pinanga* species.

Knowledge Gaps on *Pinanga* Ecology in Southeast Asia

Most studies of the genus *Pinanga* in Southeast Asia have focused on descriptive notes (Dransfield 1980; Coode *et al.* 1996; Witono *et al.* 2002; Zulkarnaen *et al.* 2019; Fernando *et al.* 2020). Although descriptive notes on *Pinanga* species are abundant (Dransfield 1980, 1991; Keat *et al.* 1998; Henderson *et al.* 2010; Fernando *et al.* 2020; Kuhnhäuser *et al.* 2023), these typically include limited information, focusing on taxonomic descriptions and brief notes on, for example, locality and habitat.

Studies that focus on population structures of *Pinanga* species are still lacking, and to date, only two studies in Southeast Asia are known to have focused on this. In Indonesia, Yudaputra *et al.* (2021) studied the population structures of *P. arinasae* in Bali Island and found that the population comprised many seedlings, but a much lower abundance of juvenile and mature individuals. Meanwhile, Zulkarnaen *et al.* (2019, 2022a) studied the population structure of *P. javana* at two sites, Mt. Ungaran and Mt. Slamet, Java, Indonesia. They found that *P. javana* populations in Mt. Ungaran mainly comprised individuals at the seedling stage (Zulkarnaen *et al.* 2019), while those at Mt. Slamet mainly comprised adult individuals with stem heights of 6.1-8.1 m and stem diameters of 7-8.9 cm (Zulkarnaen *et al.* 2022a). In Brunei Darussalam, one of the first studies of *Pinanga* was done on five *Pinanga* species (*P. aristata*, *P. brevipes*, *P. dumetosa*, *Pinanga tenella* var. *tenella*, and *P. veitchii*) by Shapcott (1999). The study compared the population genetics and densities of these five *Pinanga* species at Kuala Belalong, Brunei, and showed that all species of *Pinanga* palms studied had quite prominent levels of genetic diversity, which were correlated with population density. Shapcott (1999) further reported that the densest species had less genetic variation than less-dense species, with *P. dumetosa* exhibiting the greatest gene flow between its populations and *P. brevipes* exhibiting the lowest. The lack of studies on *Pinanga* population structure in Southeast Asia underscores the need for increased ecological investigation into the populations of these species, particularly since the region holds the highest diversity of *Pinanga* species globally. Understanding the population biology of *Pinanga* species, particularly those that are endemic to Borneo, is of priority to better inform and design management plans and conservation efforts for these palms.

Although environmental factors and soil properties have been shown to influence palm communities at different spatial scales (Eiserhardt *et al.* 2011), their influence on *Pinanga* palm communities are only beginning to be understood. Descriptives notes provide anecdotal evidence to demonstrate that *Pinanga* species display habitat preferences (Dransfield 1980; Coode *et al.* 1996; Witono *et al.* 2002; Fernando *et al.* 2020), but the significant influence of environmental factors and soil conditions still requires investigation. Although a few studies have statistically shown that *Pinanga* species appear to exhibit habitat specificity, these remain few and should be expanded to the various forest types that are known to occur throughout Borneo and in the wider Southeast Asian region. To complement investigations of drivers of *Pinanga* diversity in different forest types, an increased understanding of functional traits of *Pinanga* species, such as their growth forms, stem traits, fruit traits and leaf traits (Kissling *et al.* 2019), which could explain their habitat specificity, should also be aimed for.

It is notable that only three *Pinanga* species that are recorded as Bornean endemics have been assessed and listed in the IUCN Red List: *P. chaiana* (Near Threatened), *P. mooreana* (Least Concern) and *P. patula* (Least Concern) (IUCN 2024). *Pinanga* palms are often prized by illegal collectors and also face threats from deforestation and forest fragmentation (Bellot *et al.* 2022). The threats faced by *Pinanga* populations in Borneo and Southeast Asia highlight a need for more studies of these palms to guide the conservation management of this genus throughout the region.

CONCLUSION

It is widely accepted that palm abundance is influenced by various factors, such as climate, soil chemistry, hydrology, topography and vegetation structure. Currently available studies on the relationship between palm abundance and species richness are still lacking because not all determinants have been quantitatively studied at all scales and because some studies involved more comprehensive investigations than others. Palm species richness has been comprehensively studied only at a continental to global scale, and studies on community abundance are often conducted at local scales but less frequently at landscape to regional scales, being especially limited at a continental to global scale. Therefore, it is crucial to assess the relationship between palm abundance and species richness with biotic and abiotic factors at all spatial scales.

For *Pinanga* palms, there is still insufficient ecological understanding of the factors that act as determinants of their abundance and species richness. Studies to date have shown that *Pinanga* palms typically prefer humid conditions, thick litter layers, high canopy cover and locations near water sources, such as rivers or small streams. *Pinanga* species abundance and richness, as well as its foliar contents, can be influenced by soil properties. Detailed studies focusing on different lowland forest types with contrasting environmental conditions, and on how these factors affect *Pinanga* species abundance and richness, coupled with studies investigating their functional traits, are needed. Several *Pinanga* species are endemic to Borneo, and this highlights the need to investigate their populations and habitat preferences, particularly for the conservation of these iconic palms.

ACKNOWLEDGEMENTS

The authors would like to thank Universiti Brunei Darussalam for research funding (grant reference number: UBD/RSCH/1.13/FICBF(b)/2022/033) and the Ministry of Education, Brunei Darussalam for the lead author's graduate scholarship. We thank the Brunei Forestry Department for field and herbarium support for *Pinanga* surveys in Brunei Darussalam. We also thank Alison Shapcott and Sidonie Bellot for advice on *Pinanga* species in Brunei Darussalam.

REFERENCES

Abdo ME. 2017. A floristic study of Halmahera, Indonesia focusing on palms (Arecaceae) and their seed dispersal [Dissertation]. Retrieved from Florida International University.

Abdullah MF. 2021. Variation in foliar nutrient contents of three *Pinanga* species with contrasting habitats and leaf formations [Dissertation]. Retrieved from Universiti Brunei Darussalam archive.

Abdullah MF. 2024. Differences in diversity and communities of *Pinanga* palms in contrasting lowland tropical forests in Brunei Darussalam, Borneo [Dissertation]. Retrieved from Universiti Brunei Darussalam archive.

Adorador JT, Meneses ZD, Fernando ES. 2020. *Pinanga gruezoi* (Arecaceae), a new slender clustering palm from the Philippines with notes on an amended description of *P. samarana*. Phytotaxa [Internet]. [cited 2022 Nov 10]; 429(2):120-34. DOI: 10.11646/phytotaxa.429.2.3

Alvarado-Segura AA, Calvo-Irabién LM, Duno de Stefano R, Balslev H. 2012. Palm species richness, abundance, and diversity in the Yucatan Peninsula, in a neotropical context. Nord J Bot [Internet]. [cited 2022 Nov 10]; 30(5):613-22. DOI: 10.1111/j.1756-1051.2012.01593.x

Andersen KM, Turner BL, Dalling JW. 2010. Soil-based habitat partitioning in understorey palms in lower montane tropical forests. J Biogeogr [Internet]. [cited 2022 Nov 10]; 37(2):278-92. DOI: 10.1111/j.1365-2699.2009.02192.x

Ang WF, Lok AFSL, Tan HTW. 2010. Rediscovery in Singapore of *Pinanga simplicifrons* (Miq.) Becc. (Arecaceae). Nat Singap [Internet]. [cited 2022 Nov 18]; 3:83-6. Available from: https://lkcnhm.nus.edu.sg/app/uploads/2017/06/2010nis083-086.pdf

Astuti IW, Siswoyo S, Rustiami H. 2018. Studi Penyebaran Spasial Palem di Hutan Lindung Gunung Slamet, Jawa Tengah [Study on palm spatial distribution at Gunung Slamet Nature Forest, Central Java]. Scr biol [Internet]. [cited 2023 Jan 20]; 5(3). Available from: http://repository.ipb.ac.id/handle/123456789/61702.pdf

Bachman S, Baker WJ, Brummitt N, Dransfield J, Moat J. 2004. Elevational gradients, area, and tropical island diversity: An example from the palms of New Guinea. Ecography [Internet]. [cited 2022 Nov 10]; 27(3):299-310. DOI: 10.1111/j.0906-7590.2004.03759.x

Bacon CD, Michonneau F, Henderson AJ, Mckenna MJ, Milroy AM, Simmons MP. 2013. Geographic and taxonomic disparities in species diversity: Dispersal and diversification rates across Wallace's line. Evolution [Internet]. [cited 2022 Nov 10]; 67:2058-71. DOI: 10.1111/evo.12084

Baker WJ, Couvreur TL. 2012. Biogeography and distribution patterns of Southeast Asian palm. In: Gower DJ, Johnson KG, Richardson JE, Rüber L, Williams ST (Editors). Biotic Evolution and Environmental Change in Southeast Asia. New York (US): Cambridge University Press.

Baker WJ, Couvreur TL. 2013. Global biogeography and the diversification of palms shed light on the evolution of tropical lineages. I. Historical biogeography. J Biogeogr [Internet]. [cited 2022 Nov 10]; 40(2):274-85. DOI: 10.1111/j.1365-2699.2012.02795.x

Baker WJ, Dransfield J. 2016. Beyond *Genera Palmarum*: Progress and prospects in palm systematics. Bot J Linn [Internet]. [cited 2022 Nov 10]; 182(2):207-33. DOI: 10.1111/boj.12401

Balslev H, Bernal R, Fay MF. 2016. Palms–emblems of tropical forests. Bot J Linn [Internet]. [cited 2022 Nov 10]; 182(2):195-200. DOI: 10.1111/boj.12465

Balslev H, Kahn F, Millan B, Svenning JC, Kristiansen T, Borchsenius F, … Eiserhardt WL. 2011. Species diversity and growth forms in tropical American palm communities. Bot Rev [Internet]. [cited 2022 Nov 10]; 77(4):381-425. DOI: 10.1007/s12229-011-9084-x

Balslev H, Luteyn J, Øllgaard B, Holm-Nielsen LB. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. Opera bot [Internet]. [cited 2022 Nov 10]; 92:37-57. Available from: https://www.researchgate.net/publication/284041002_Composition_and_structure_of_adjacent_unflooded_and_floodplain_forest_in_Amazonian_Ecuador.pdf

Baribault TW, Kobe RK, Finley AO. 2012. Tropical tree growth is correlated with soil phosphorus, potassium, and calcium, though not for legumes. Ecol Monogr [Internet]. [cited 2023 Jan 2]; 82(2):189-203. Available from: http://www.jstor.org/stable/41739364.pdf

Bellot S, Lu Y, Baker WJ, Dransfield J, Forest F, Kissling WD, … Bachman SP. 2022. The likely extinction of hundreds of palm species threatens their contributions to people and ecosystems. Nat. Ecol. Evol. [Internet]. [cited 2024 July 1]; 6(11):1710-22. DOI: 10.1038/s41559-022-01858-0

Benchimol M, Talora DC, Mariano-Neto E, Oliveira TL, Leal A, Mielke MS, Faria D. 2017. Losing our palms: The influence of landscape-scale deforestation on Arecaceae diversity in the Atlantic forest. For Ecol Manag [Internet]. [cited 2023 Jan 2]; 384:314-22. DOI: 10.1016/j.foreco.2016.11.014

Bjorholm S, Svenning JC, Baker WJ, Skov F, Balslev H. 2006. Historical legacies in the geographical diversity patterns of New World palm (Arecaceae) subfamilies. Bot J Linn [Internet]. [cited 2022 Nov 10]; 151(1):113-25. DOI: 10.1111/j.1095-8339.2006.00527.x

Bjorholm S, Svenning JC, Skov F, Balslev H. 2005. Environmental and spatial controls of palm (Arecaceae) species richness across the Americas. Glob Ecol Biogeogr [Internet]. [cited 2022 Nov 10]; 14(5):423-9. DOI: 10.1111/j.1466-822x.2005.00167.x

Blach-Overgaard A, Svenning JC, Dransfield J, Greve M, Balslev H. 2010. Determinants of palm species distributions across Africa: The relative roles of climate, non-climatic environmental factors, and spatial constraints. Ecography [Internet]. [cited 2022 Nov 10]; 33(2):380-91. DOI: 10.1111/j.1600-0587.2010.06273.x

Bogota-Angel G, Huang H, Jardine PE, Chazot N, Salamanca S, Banks H, Hoorn C. 2021. Climate and geological change as drivers of Mauritiinae palm biogeography. J Biogeogr [Internet]. [cited 2022 Nov 10]; 48(5):1001-22. DOI: 10.1111/jbi.14098

Bonetti S, Feng X, Porporato A. 2017. Ecohydrological controls on plant diversity in tropical South America: Ecohydrological controls on plant diversity. Ecohydrol [Internet]. [cited 2022 Nov 10]; 10:e1853. DOI: 10.1002/eco.1853

Boukili VK, Chazdon RL. 2017. Environmental filtering, local site factors, and landscape context drive changes in functional trait composition during tropical forest succession. PPEES [Internet]. [cited 2023 Dec 7]; 24:37-47. DOI: 10.1016/j.ppees.2016.11.003

Browne L, Karubian J. 2016. Diversity of palm communities at different spatial scales in a recently fragmented tropical landscape. Bot J Linn 182 [Internet]. [cited 2022 Nov 10]; (2):451-64. DOI: 10.1111/boj.12384

Cámara-Leret R, Faurby S, Macía MJ, Balslev H, Göldel B, Svenning JC, … Saslis-Lagoudakis CH. 2017a. Fundamental species traits explain the provisioning services of tropical American palms. Nat Plants [Internet]. [cited 2022 Nov 10]; 3(2):1-7. DOI: 10.1038/nplants.2016.220

Cámara-Leret R, Tuomisto H, Ruokolainen K, Balslev H, Munch Kristiansen S. 2017b. Modelling responses of western Amazonian palms to soil nutrients. J Ecol [Internet]. [cited 2022 Nov 10]; 105(2):367-81. DOI: 10.1111/1365-2745.12708

Carson W, Schnitzer S (Editors). 2011. Tropical Forest Community Ecology. New York (US): Wiley-Blackwell.

Cintra R, Ximenes ADC, Gondim FR, Kropf MS. 2005. Forest spatial heterogeneity and palm richness, abundance and community composition in Terra Firme forest, Central Amazon. Rev Bras Bot [Internet]. [cited 2022 Nov 10]; 28:75-84. DOI: 10.1590/S0100-84042005000100007

Condit R, Engelbrecht BM, Pino D, Pérez R, Turner BL. 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. PNAS [Internet]. [cited 2022 Nov 10]; 110(13):5064-8. DOI: 10.1073/pnas.1218042110

Coode MJE, Kirkup DW, Dransfield J, Forman LL, Said IM. 1996. A checklist of the flowering plants and gymnosperms of Brunei Darussalam. Bandar Seri Begawan (BN): Ministry of Industry and Primary Resources.

Couvreur TL, Baker WJ. 2013. Tropical rain forest evolution: Palms as a model group. BMC Biology [Internet]. [cited 2022 Nov 10]; 11(1):1-4. DOI: 10.1186/1741-7007-11-48

Dalling JW, Heineman K, González G, Ostertag R. 2016. Geographic, environmental, and biotic sources of variation in the nutrient relations of tropical montane forests. J Trop Ecol [Internet]. [cited 2022 Nov 10]; 32(5):368-83. DOI: 10.1017/S0266467415000619

Dransfield J, Uhl NW, Asmussen CB, Baker WJ, Harley MM, Lewis CE. 2008. Genera Palmarum: The Evolution and Classification of Palms. London (UK): Kew Royal Botanic Gardens.

Dransfield J. 1980. Systematic notes on *Pinanga* (Palmae) in Borneo. Kew Bulletin [Internet]. [cited 2024 June 10]; 769-788. DOI: 10.2307/4119070

Dransfield J. 1991. Notes on *Pinanga* (Palmae) in Sarawak. Kew Bulletin [Internet]. [cited 2024 June 10]; 691-8. DOI: 10.2307/4110412

Eiserhardt WL, Svenning JC, Kissling WD, Balslev H. 2011. Geographical ecology of the palms (Arecaceae): Determinants of diversity and distributions across spatial scales. Ann Bot [Internet]. [cited 2022 Nov 10]; 108(8):1391-416. DOI: 10.1093/aob/mcr146

Elias GA, Gasper AL, Lima JMT, Soares KP, Molz M, Santos R. 2016. Community structure of large native arborescent palms (Arecaceae) using data from the Floristic and Forest Inventory of Santa Catarina, Brazil. Int J Basic Appl Sci [Internet]. [cited 2022 Dec 7]; 10(10):156-63. DOI: 10.13140/RG.2.2.32588.21124

Elias GA, Giehl ELH, De Gasper AL, Lima JMT, Dos Santos R. 2019. Low-temperature extremes influence both the presence of palms and palm species richness in the Atlantic Forest, Southern Brazil. Ecol Austral [Internet]. [cited 2022 Dec 7]; 29(1):041-9. Available from: https://www.academia.edu/82650348/Low_temperature_extremes_influence_both_the_presence_of_palms_and_palm_species_richness_in_the_Atlantic_Forest_Southern_Brazil?f_ri=377014.pdf

Emilio T, Quesada CA, Costa FR, Magnusson WE, Schietti J, Feldpausch TR, Phillips OL. 2014. Soil physical conditions limit palm and tree basal areas in Amazonian forests. Plant Ecol Divers [Internet]. [cited 2022 Dec 7]; 7(1-2):215-29. DOI: 10.1080/17550874.2013.772257

Fernando ES, Logatoc ELR, Malabrigo PLJr, Adorador JT. 2020. *Pinanga lepidota* (Arecaceae: Arecoideae), a new record for the Philippines from Palawan Island. Philipp J Syst Biol [Internet]. [cited 2022 Nov 18]; 14(3):1-6. Available from: https://10.26757/pjsb2020c14005

Gatti MG, Campanello PI, Montti LF, Goldstein G. 2008. Frost resistance in the tropical palm *Euterpe edulis* and its pattern of distribution in the Atlantic Forest of Argentina. For Ecol Manag [Internet]. [cited 2022 Nov 10]; 256(4):633-40. DOI: 10.1016/j.foreco.2008.05.012

Göldel B, Kissling WD, Svenning JC. 2015. Geographical variation and environmental correlates of functional trait distributions in palms (Arecaceae) across the New World. Bot J Linn [Internet]. [cited 2022 Dec 20]; 179(4):602-17. DOI: 10.1111/boj.12349

Goodman RC, Phillips OL, del Castillo Torres D, Freitas L, Cortese ST, Monteagudo A, Baker TR. 2013. Amazon palm biomass and allometry. For Ecol Manag [Internet]. [cited 2022 Nov 10]; 310:994-1004. DOI: 10.1016/j.foreco.2013.09.045

Govaerts R, Dransfield J, Zona S, Hodel DR, Henderson A. 2020. World Checklist of Arecaceae. Facilitated by the Royal Botanic Gardens, Kew [Internet]. [cited 2022 Nov 10]. Available from: http://apps.kew. org/wcsp/

Haji Ramlan NS. 2020. The influence of soil properties on *Pinanga* palms at two contrasting Mixed Dipterocarp forests in Brunei Darussalam [Dissertation]. Retrieved from Universiti Brunei Darussalam archive.

Hawkins B, Field R, Cornell H, Currie D. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology [Internet]. [cited 2022 Nov 10]; 84:3105-17. DOI: 10.1890/03-8006

Henderson A, Ban NK, Thanh BV. 2010. New species of *Areca*, *Pinanga* and *Licuala* (Arecaceae) from Vietnam. Phytotaxa [Internet]. [cited 2023 Feb 1]; 8(1):34-40. DOI: 10.11646/phytotaxa.8.1.3

Henderson A, Galeano G, Bernal R. 2019. A Field Guide to the Palms of the Americas (Vol. 5390). New Jersey (US): Princeton University Press.

Henderson A, Dung NQ. 2017. New species of *Lanonia*, *Licuala* and *Pinanga* (Arecaceae) from Vietnam. Phytotaxa [Internet]. [cited 2023 Feb 1]; 323(2):159-72. DOI: 10.11646/phytotaxa.323.2.4

Hilário RR, Toledo JJ. 2016. Effects of climate and forest structure on palms, bromeliads and bamboos in Atlantic Forest fragments of Northeastern Brazil. Braz J Biol [Internet]. [cited 2022 Nov 10]; 76:834-44. DOI: 10.1590/1519-6984.00815

Iryadi R, Sutomo S. 2020. Autecology of an endemic palm *Pinanga arinasae* JR Witono in Bali, Indonesia. J Trop Biodiv Biotech [Internet]. [cited 2022 Nov 18]; 5(2):108-14. DOI: 10.22146/jtbb.54650

IUCN. 2024. The IUCN Red List of Threatened Species. Version 2024-1 [Internet]. [cited 2024 July 1]. Available from: https://www.iucnredlist.org/

John R, Dalling JW, Harms KE, Yavitt JB, Stallard RF, Mirabello M, … Foster RB. 2007. Soil nutrients influence the spatial distributions of tropical tree species. PNAS [Internet]. [cited 2022 Nov 10]; 104:864-9. DOI: 10.1073/pnas.0604666104

Kahn F, de Castro A. 1985. The palm community in a forest of central Amazonia, Brazil. Biotropica [Internet]. [cited 2022 Nov 10]; 210-6. DOI: 10.2307/2388221

Kahn F. 1987. The distribution of palms as a function of local topography in Amazonian terra-firme forests. Experientia Basel [Internet]. [cited 2022 Nov 10]; 43(3):251-8. DOI: 10.1007/BF01945548

Keat LC, Dransfield J, Kiew R, Guan SL. 1998. Four new *Pinanga* Blume (Palmae) species from Peninsular Malaysia. Gardens' Bulletin Singapore [Internet]. [cited 2024 June 10]; 50:99-114. Available from: https://www.nparks.gov.sg/sbg/research/publications/gardens-bulletin-singapore/-/media/sbg/gardens-bulletin/4-4-50-1-10-y1998-v50p1-gbs-pg-99.pdf

Kissling WD, Balslev H, Baker WJ, Dransfield J, Göldel B, Lim JY, … Svenning JC. 2019. PalmTraits 1.0, a species-level functional trait database of palms worldwide. Sci Data [Internet]. [cited 2022 Nov 10]; 6(1):1-13. DOI: 10.1038/s41597-019-0189-0

Kissling WD, Eiserhardt WL, Baker WJ, Borchsenius F, Couvreur TL, Balslev H, Svenning JC. 2012. Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. PNAS [Internet]. [cited 2022 Nov 10]; 109(19):7379-84. DOI: 10.1073/pnas.1120467109

Kreft H, Jetz W. 2007. Global patterns and determinants of vascular plant diversity. PNAS [Internet]. [cited 2022 Nov 10]; 104(14):5925-30. DOI: 10.1073/pnas.0608361104

Kreft H, Sommer JH, Barthlott W. 2006. The significance of geographic range size for spatial diversity patterns in Neotropical palms. Ecography [Internet]. [cited 2022 Nov 10]; 29(1):21-30. DOI: 10.1111/j.2005.0906-7590.04203.x

Kristiansen T, Svenning JC, Eiserhardt WL, Pedersen D, Brix H, Munch Kristiansen S, … Balslev H. 2012. Environment versus dispersal in the assembly of western Amazonian palm communities. J Biogeogr [Internet]. [cited 2022 Nov 10]; 39(7):1318-32. DOI: 10.1111/j.1365-2699.2012.02689.x

Kristiansen T, Svenning JC, Pedersen D, Eiserhardt WL, Grández C, Balslev H. 2011. Local and regional palm (Arecaceae) species richness patterns and their cross-scale determinants in the western Amazon. J Ecol [Internet]. [cited 2022 Nov 10]; 99(4):1001-15. DOI: 10.1111/j.1365-2745.2011.01834.x

Kuhnhäuser BG, Randi A, Petoe P, Chai PP, Bellot S, Baker WJ. 2023. Hiding in plain sight: The underground palm *Pinanga subterranea*. Plants, People, Planet [Internet]. [cited 2024 June 10]; 5(6), 815-20. DOI: 10.1002/ppp3.10393

Levis C, Costa FR, Bongers F, Peña-Claros M, Clement CR, Junqueira AB, Sandoval EV. 2017. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. Sci [Internet]. [cited 2022 Dec 7]; 355(6328):925-31. DOI: 10.1126/science.aal0157

Lieberman D, Lieberman M, Peralta R, Hartshorn GS. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. J Ecol [Internet]. [cited 2022 Nov 10];137-52. DOI: 10.2307/2261350

Lim J, Chong R, Chia Z, Jinying T, Foong AW. 2022. Biodiversity Record: New locality record for the palm, *Pinanga simplicifrons*, in Singapore. Nat Singap [Internet]. [cited 2023 Feb 1]; 15:e2022042. Available from: https://

lkcnhm.nus.edu.sg/wpcontent/uploads/sites/10/2022/04/NIS-2022-0043.pdf

Limin A, Slik F, Sukri RS, Chen SB, Ahmad JA. 2022. Large tree species composition, not growth rates, is affected by topography in a Bornean tropical forest. Biotropica [Internet]. [cited 2023 Apr 20]; 53(5):1290-300. DOI: 10.1111/btp.12969

Loo AHB, Ang WF, Baker WJ, Tan HTW. 2014. A Guide to the Native Palms of Singapore. Singapore (SG): Singapore Science Centre.

Lueder S. 2020. Palm community diversity and composition in a tropical human-modified landscape [Dissertation]. Retrieved from Tulane University.

Macedo-Santana F, Flores-Tolentino M, Hernández-Guzmán R. 2021. Diversity patterns of palms in Mexico using species distribution models. Écoscience [Internet]. [cited 2022 Nov 10]; 28(2):137-47. DOI: 10.1080/11956860.2021.1888522

Mainasara MM, Bakar MA, Linatoc AC. 2019. Cytotoxic activities of *Pinanga limosa* (Pinang Puteri) from Endau Rompin Johor, Malaysia. In: IOP Conference Series: Earth and Environmental Science. 11-13 November 2018.

Manggat MA. 2012. Influence of altitude on distribution of native palm species: A case study at Gunung Jagoi, Bau, Sarawak [Dissertation]. Retrieved from Universiti Malaysia Sarawak.

Martins RC, Filgueiras TDS, Albuquerque UP. 2014. Use and diversity of palm (Arecaceae) resources in central-western Brazil. Sci World J [Internet]. [cited 2023 Feb 2]; 2014. DOI: 10.1155/2014/942043

Mehmud S, Roy H. 2021. Diversity and distribution of palms (Arecaceae) in Assam, India. Check List [Internet]. [cited 2023 Feb 2]; 17(1):69-93. DOI: 10.15560/17.1.69

Moeslund JE, Arge L, Bøcher PK, Dalgaard T, Svenning JC. 2013. Topography as a driver of local terrestrial vascular plant diversity patterns. Nord J Bot [Internet]. [cited 2023 Feb 2]; 31(2):129-44. DOI: 10.1111/j.1756-1051.2013.00082.x

Montoya F, Mónica MR, Fuentes AF, Cayola L, Antezana A, Miranda T, … Tello JS. 2021. Relative effects of edaphic conditions and climate on palm communities in the Central Andes. bioRxiv [Internet]. [cited 2022 Nov 10]. DOI: 10.1101/2021.03.08.434423

Montúfar R, Anthelme F, Pintaud JC, Balslev H. 2011. Disturbance and resilience in tropical American palm populations and communities. Bot Rev [Internet]. [cited 2022 Nov 10]; 77:426-61. DOI: 10.1007/s12229-011-9085-9

Montúfar R, Pintaud JC. 2006. Variation in species composition, abundance, and microhabitat preferences among western Amazonian terra firme palm communities. Biol J Linn Soc [Internet]. [cited 2022 Nov 10]; 151(1):127-40. DOI: 10.1111/j.1095-8339.2006.00528.x

Mooney M. 2020. Landscape distribution of *Pinanga* palm (Arecaceae) species in Brunei Darussalam [Dissertation]. Retrieved from The University of the Sunshine Coast.

Moraes MR, Ríos-Uzeda B, Moreno LR, Huanca-Huarachi G, Larrea-Alcázar D. 2014. Using potential distribution models for patterns of species richness, endemism, and phytogeography of palm species in Bolivia. Trop Conserv Sci [Internet]. [cited 2022 Nov 10]; 7(1):45-60. DOI: 10.1177/194008291400700109

Muscarella R, Emilio T, Phillips OL, Lewis SL, Slik F, Baker WJ, Poedjirahajoe E. 2020. The global abundance of tree palms. Glob Ecol Biogeogr [Internet]. [cited 2022 Nov 10]; 29(9):1495-514. DOI: 10.1111/geb.13123

Normand S, Vormisto J, Svenning JC, Grandez C, Balslev H. 2006. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. Plant Ecol [Internet]. [cited 2022 Nov 10]; 186(2):161-76. DOI: 10.1007/s11258-006-9120-9

Odufuwa P. 2019. DNA barcoding of *Pinanga* (Arecaceae) of Borneo [Dissertation]. Retrieved from The University of London.

Onstein RE, Baker WJ, Couvreur TL, Faurby S, Svenning JC, Kissling WD. 2017. Frugivory-related traits promote the speciation of tropical palms. Nat Ecol Evol [Internet]. [cited 2022 Nov 10]; 1(12):1903-11. DOI: 10.1038/s41559-017-0348-7

Pasion BO, Duya MRM, Ong PS, Fernando ES. 2022. Twelve-year changes in palm populations from a tropical lowland forest in the Philippines. Community Ecol [Internet]. [cited 2023 Feb 2]; 23:327-35. DOI: 10.1007/s42974-022-00109-3

Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr [Internet]. [cited 2022 Nov 10]; 12(5):361-71. DOI: 10.1046/j.1466-822X.2003.00042.x

Poulsen AD, Tuomisto H, Balslev H. 2006. Edaphic and floristic variation within a 1-ha plot of lowland Amazonian rain forest 1. Biotropica [Internet]. [cited 2022 Nov 10]; 38(4):468-78. DOI: 10.1111/j.1744-7429.2006.00168.x

POWO. 2024. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. [Internet]. [cited 2024 July 1]; Available from: http://www.plantsoftheworldonline.org/

Randi A, Hikmat A, Heatubun CD. 2019. *Pinanga schwanerensis*, a new species of *Pinanga* (Arecaceae) from Kalimantan, Indonesia. Phytotaxa [Internet]. [cited 2022 Nov 18]; 402(2):121-5. DOI: 10.11646/phytotaxa.402.2.6

Reichgelt T, West CK, Greenwood DR. 2018. The relation between global palm distribution and climate. Scientific Reports [Internet]. [cited 2023 Feb 2]; 8(1):1-11. DOI: 10.1038/s41598-018-23147-2

Renninger HJ, Phillips NG. 2016. Palm physiology and distribution in response to global environmental change. In: Goldstein G, Santiago LS (Editors). Tropical Tree Physiology Vol. 6. Cham (CH): Springer International Publishing

Rodrigues LF, Cintra R, Castilho CV, de Sousa Pereira O, Pimentel TP. 2014. Influences of forest structure and landscape features on spatial variation in species composition in a palm community in central Amazonia. J Trop Ecol [Internet]. [cited 2023 Feb 2]; 30(6):565-78. DOI: 10.1371/journal.pone.0171540

Ruokolainen K, Vormisto J. 2000. The most widespread Amazonian palms tend to be tall and habitat generalists. Appl Soil Ecol [Internet]. [cited 2022 Nov 10]; 1(2):97-108. DOI: 10.1078/1439-1791-00020

Salm R, Prates A, Simoes NR, Feder L. 2015. Palm community transitions along a topographic gradient from floodplain to terra firme in the eastern Amazon. Acta amazônica [Internet]. [cited 2022 Nov 10]; 45:65-74. DOI: 10.1590/1809-4392201401533

Salm R, Salles NVD, Alonso WJ, Schuck-Paim C. 2007. Cross-scale determinants of palm species distribution. Acta amazónica [Internet]. [cited 2022 Nov 10]; 37(1):17-25. DOI: 10.1590/S0044-59672007000100002

Sanders NJ, Rahbek C. 2012. The patterns and causes of elevational diversity gradients. Ecography [Internet]. [cited 2022 Nov 10]; 35(1):1. DOI: 10.2307/41406206

Scariot AO. 2015. Palmeiras brasileiras: botânica, ecologia, usos e conservação. In: Lopes R, Oliveira MSP, Cavallari MM, Barbieri RL, Conceição LDHCS (Editors). Palmeiras nativas do Brasil. Brasília (BR): Embrapa. p. 15-33.

Sevegnani LA, Uhlmann AL, Gasper L, Meyer L, Vibrans AC. 2016. Climate affects the structure of mixed rain forests in the southern sector of the Atlantic domain in Brazil. Acta Oecologica [Internet]. [cited 2023 Feb 2]; 77:109-77. DOI: 10.1016/j.actao.2016.10.002

Shapcott A, Slik F, Rosli R, Sukri RS. 2022. *Pinanga* palms revisited 20 years on: what can changes in *Pinanga* species populations tell us about rainforest understory palm persistence? J Trop Ecol [Internet]. [cited 2023 Feb 2]; 38(6):351-61. DOI: 10.1017/S0266467422000256

Shapcott A. 1999. Comparison of the population genetics and densities of five *Pinanga* palm species at Kuala Belalong, Brunei. Mol Ecol [Internet]. [cited 2022 Nov 18]; 8(10):1641-54. DOI: 10.1046/j.1365-294x.1999.00749.x

Siebert SF. 2005. The abundance and distribution of rattan over an elevation gradient in Sulawesi, Indonesia. For Ecol Manag [Internet]. [cited 2022 Nov 10]; 210(1-3):143-58. DOI: 10.1016/j.foreco.2005.02.015

Sørensen MV. 2012. Determinants of the distribution ranges of eleven economically important palm species in western South America [Dissertation]. Retrieved from Aarhus University.

Sukri RS, Wahab RA, Salim KA, Burslem DF. 2012. Habitat associations and community structure of dipterocarps in response to environment and soil conditions in Brunei Darussalam, Northwest Borneo. Biotropica [Internet]. [cited 2023 Apr 20]; 44(5):595-605. DOI: 10.1111/j.1744-7429.2011.00837.x

Sutomo S, Darma IDP, Sujarwo W, Priyadi A, Kuswantoto F, Iryadi R. 2018. Ecology of Bedugul Basin Bali. Bogor (ID): SEAMEO BIOTROP.

Svenning JC, Borchsenius F, Bjorholm S, Balslev H. 2008. High tropical net diversification drives the New World latitudinal gradient in the palm (Arecaceae) species richness. J Biogeogr [Internet]. [cited 2022 Nov 10]; 35(3):394-406. DOI: 10.1111/j.1365-2699.2007.01841.x

Svenning JC. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. J Ecol [Internet]. [cited 2022 Nov 10]; 87(1):55-65. DOI: 10.1046/j.1365-2745.1999.00329.x

Svenning JC. 2000. Growth strategies of clonal palms (Arecaceae) in a neotropical rainforest, Yasuni, Ecuador. Aust J Bot [Internet]. [cited 2022 Nov 10]; 48(2):167-78. DOI: 10.1071/BT98048

Svenning JC. 2001. On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). Bot Rev [Internet]. [cited 2022 Nov 10]; 67(1):1-53. DOI: 10.1007/BF02857848

Syahida-Emiza S, Syazwani A, Rafidah AR, Nor-Ezzawanis AT, Ummul-Nazrah AR. 2018. Heart of Borneo: Exploring the beauty of Long Banga. Conservation Malaysia [Internet]. [cited 2022 Nov 18]. Available from https://www.mybis.gov.my/pd/283.pdf

Syauqina MY, Meekiong K, Aimi Syazana S, Miraadila MI. 2017. Diversity of palms in Dered Krian National Park, Bau. In: Meekiong K, Azahari O, Pungga RS, Wasli ME, Freddy YKS, Marconi SJ (Editors). Proceedings of Colloquium on the Dered Krian National Park-Scientific Expedition 2016. Kuching, Sarawak. p. 15-9.

Thonhofer J, Getto D, van Straaten O, Cicuzza D, Kessler M. 2015. Influence of spatial and environmental variables on rattan palm (Arecaceae) assemblage composition in Central Sulawesi, Indonesia. Plant Ecol [Internet]. [cited 2022 Nov 10]; 216(1):55-66. DOI: 10.1007/s11258-014-0416-x

Viana JL, Turner BL, Dalling JW. 2021. Compositional variation in understorey fern and palm communities along a soil fertility and rainfall gradient in a lower montane tropical forest. J Veg Sci [Internet]. [cited 2023 Feb 5]; 32(1):e12947. DOI: 10.1111/jvs.12947

Vormisto J, Svenning JC, Hall P, Balslev H. 2004. Diversity and dominance in the palm (Arecaceae) communities in terra firme forests in the western Amazon basin. J Ecol [Internet]. [cited 2022 Nov 10]; 92(4):577-88. DOI: 10.1111/j.0022-0477.2004.00904.x

Wahyuni AS, Prasetyo LB, Zuhud EA. 2017. Population and distribution plant pattern Paliasa (*Kleinhovia hospita* L.) in Bontobahari District. Media Konservasi [Internet]. [cited 2023 Feb 7]; 22(1):11-8. DOI: 10.29244/medkon.22.1.11-18

Wang B, Zhang G, Duan J. 2015. Relationship between topography and the distribution of understory vegetation in a *Pinus massoniana* forest in Southern China. ISWCR [Internet]. [cited 2023 Feb 2]; 3(4):291-304. DOI: 10.1016/j.iswcr.2015.10.002

Witono JR, Mogea JP, Somadikarta S. 2002. *Pinanga* in Java and Bali. Palms [Internet]. [cited 2022 Nov 18] 46:193-201. Available from: https://www.academia.edu/24062744/Pinanga_in_Java_and_Bali.pdf

Yudaputra A, Rahardjo P. 2020. Short Communication: Plant species richness and diversity in Karangsambung-Karangbolong National Geopark, Indonesia. Biodiversitas [Internet]. [cited 2022 Nov 10]; 21(4):1735-42. DOI: 10.13057/biodiv/d210457

Yudaputra A, Witono JR, Astuti IP, Munawaroh E, Fijridiyanto IA, Zulkarnaen RN, … Cropper WP. 2021. Habitat suitability, population structure and conservation status of *Pinanga arinasae* (Arecaceae), an endemic palm in Bali Island, Indonesia. Diversity [Internet]. [cited 2022 Nov 18]; 14(1):10. DOI: 10.3390/d14010010

Zulkarnaen RN, Helmanto H, Wihermanto W, Primananda E, Robiansyah I, Kusuma YWC. 2022a. Population study of endemic Java palm *Pinanga javana* in Mount Ungaran, Semarang, Central Java, Indonesia. Biosaintifika: J Biol Educ [Internet]. [cited 2022 Nov 18]; 14(1):48-56. DOI: 10.15294/biosaintifika.v14i1.35230

Zulkarnaen RN, Helmanto H, Fikriyya N, Witono JR. 2022b. Palm species diversity on Mount Slamet, Central Java, Indonesia. In: IOP Conference Series: Earth and Environmental Science (Vol. 976, No. 1, p. 012048). IOP Publishing.

Zulkarnaen RN, Nisyawati N, Witono JR. 2019. Population study and habitat preferences of Pinang Jawa (*Pinanga javana*) in Mt. Slamet, Central Java, Indonesia. Biodiversitas [Internet]. [cited 2022 Nov 18]; 20(3):712-8. DOI: 10.13057/biodiv/d200314

Zulkarnaen RN, Nisyawati N, Witono JR. 2020. The growth and distribution pattern of endemic Java palm (*Pinanga javana* Blume) in Mt. Slamet, Central Java, Indonesia. In: AIP Conference Proceedings (Vol. 2231, No. 1). AIP Publishing.