

Impacts of invasive tree species *Bellucia pentamera* on plant diversity, microclimate and soil of secondary tropical forest in West Sumatra, Indonesia

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Abstract. Solfiyeni, Syamsuardi, Chairul, Mukhtar E. 2022. Impacts of invasive tree species *Bellucia pentamera* on plant diversity, microclimate and soil of secondary tropical forest in West Sumatra, Indonesia. *Biodiversitas* 23: 3135-3146. The invasion of alien species in a region can alter species diversity. *Bellucia pentamera* Naudin is considered an alien invasive plant that has spread from Mexico to tropical America, and it is now invading some areas in Indonesia, including the tropical forest of Sumatra. Yet, the effects of its invasion on vegetation and the abiotic environment are not yet well understood. The objective of this study was to investigate the impacts of *B. pentamera* on species diversity and structure of vegetation, and microclimate and soil conditions of secondary tropical forests in West Sumatra. Vegetation analysis was conducted in secondary forest Bukit Tengah Pulau, South Solok, with three levels of dominance of *B. pentamera* namely: site 1 and 2 (60% and 16% dominance of *B. pentamera* respectively) and site 3 (no individual of *B. pentamera*). Sampling was conducted using a nested plot to collect data for tree, sapling and understorey vegetation for each site. The results showed the total number of tree species at sites 1, 2, and 3 were 23 species, 46 species, and 74 species respectively. For sapling, 20 species were found at site 1, 31 species at site 2, and 58 species at site 3. For understorey plants, 13, 16 and 36 species were detected at site 1, 2 and 3 respectively. The number of species at tree and sapling levels differed significantly among sites. The basal area also differed significantly among sites but not for sapling level. Site 1 was dominated by *B. pentamera* with Important Value Index (IVI) 130.8%, followed by *Croton argyratus* (27.63%), and *Ficus variegata* (26.47%). At site 2, *B. pentamera* dominated with IVI of 33.68%, followed by *Lepisanthes* sp. (20.01%) and *Sizygium* sp. (14.44%). Site 3 was dominated by *Palaquium warsurifolium* with IVI of 21.15% followed by *Croton argyratus* (20.02%) and *Macaranga hypoleuca* (13.21%). Diversity index (H') for tree-level was moderate at site 1 ($H' = 1.78$) and high at sites 2 and 3 ($H' = 3.48$ and 4.05). Similarly, the index for sapling was moderate at site 1 ($H' = 2.12$) and high at sites 2 and 3 ($H' = 3.22$ and 3.84). For understorey, the diversity index was low at site 1 ($H' = 0.82$) and moderate at sites 2 and 3 ($H' = 1.8$ and 2.86). Sites invaded by *B. pentamera* had a lower soil water content and higher temperature and light intensity, although they had higher nitrogen and phosphorus contents. Our findings suggest that the invasion of *B. pentamera* had negative impacts on plant biodiversity and microclimate, yet the impact was not clear cut on the soil.

Keywords: *Bellucia pentamera*, invasive plant, microclimate, secondary forest, structure and composition

INTRODUCTION

Deforestation causes loss of forest cover which changes flora and fauna habitats and results in loss of biodiversity and triggers wildlife and human conflicts (Chakravarty et al. 2012). Many conservation efforts and floral regeneration assessments have been made to improve damaged ecosystems (Ghimire and Lamichhane 2020; Mohammadi et al. 2014). However, the damaged forests can regenerate themselves depending on the scale of the damage. For example, forests damaged by selective logging can restore more quickly than the damage caused by forest clearing and burning for plantations and agriculture. One of the factors causing the slow vegetation succession in disturbed forests is due to the presence of invasive plants (Ashton et al. 2001). Invasive plant species are either indigenous or non-indigenous species that can heavily colonize a particular habitat. Alien species are non-native or exotic organisms that disperse and adapt outside their biogeographical origin. They are also widely distributed in all kinds of ecosystems throughout the world.

Invasive alien species (IAS) are now affecting every ecosystem type on the planet and they are considered the second greatest global threat to biodiversity after habitat destruction (Shiferaw et al. 2018; Convention on Biodiversity 2015).

Alien plant species have been introduced by humans all over the globe and many of them have become invasive. They have modified ecosystems for centuries with great effects on the environment and human well-being. The number of alien invasive plant species continues to increase along with the development of agriculture, forestry, and industry and this increase is not yet saturated (Milanović et al. 2020). More than 2000 exotic plant species are widely spread in Indonesia and more than 300 have been identified as invasive (Setyawati et al. 2015). Alien species' entrance into a country might happen intentionally or accidentally. Alien plant species were introduced to Indonesia for cultivation, as experimental and curiosities, or through a botanic garden's collection. The alien species might also be imported through plant propagules infecting imported agricultural products. The species could be useful or have a

possibility as invasive. Botanic gardens (BGs) have been implicated in the early cultivation of most environmental weeds listed by the International Union for Conservation of Nature and Natural Resources (IUCN), and some of their living collections have been argued as alien weeds (Lestari 2021).

Non-native invasive plant species tend to grow faster than co-occurring native species, even in low-resource habitats (Heberling and Fridley 2016). According to Qi et al. (2014), invasive alien species can change the structure and diversity of plant communities by suppressing subordinate species. Each invading plant causes a large reduction in species richness at a small scale, although it drives a much smaller proportional reduction in species richness at a large scale (Powell et al. 2013). Stohlgren and Rejmánek (2014) found that the impact of invasion is not universal, but varies in space and time depending on the nature of the species. Many studies have also shown that invasive species can alter ecosystem functioning. Direct effects of invaders on ecosystem functioning could arise through alterations in disturbance regimes or nutrient levels. Indirect effects of biodiversity loss will only be important in comparison if invaders strongly reduce biodiversity and if biodiversity strongly affects functioning. Invasive species might therefore affect ecosystem functioning in-directly through changes in plant diversity, plant biomass or both, i.e. a loss of plant diversity reduces biomass production and other functions in turn (Linders et al. 2019).

Invasiveness is highly affected by habitat disturbances (Lozon and MacIsaac 1997), where changes in the microclimate provide a suitable environment for the occurrence of pioneer plant species as well as invasive ones. In forest ecosystems, threats posed by IAS include resource competition, hybridization and disease transmission (Langmaier and Lapin 2020). Countries with high deforestation rates, such as Indonesia (Hansen et al. 2013; Margono et al. 2012; Margono et al. 2014), have been invaded by various invasive species. The loss of tree canopy impacts the microclimate on the forest floor, such as increased light intensity, increased room temperature, and rapid groundwater loss. Forest organisms living below or within tree canopies experience distinct climatic conditions that deviate considerably from the climate outside forests. Below forest canopies, direct sunlight and wind speed are strongly reduced, leading to a dampening of temperature and humidity variations. Microclimates influence an organism's physiology, activity patterns, behavior, and fitness (De Frenne et al. 2021).

Invasive plants increased soil N availability by producing more litter that was N enriched. Invasive plants enhance the N cycle by increasing N flow to the soil through greater litter N production and litter N content, and increasing available soil N uptake, through the production of larger fine roots and specific root lengths. (Jo et al. 2017). However, local species such as pioneer species and several climax species also vary in their adaptability to environmental changes (Dong et al. 2013; Philipson et al. 2012). It means that areas invaded by invasive species can also be filled by various local species whose variations can

depend on the dominance of the invasive species and the ability of local species to adapt. Plant invasions alter abiotic components of the ecosystem in many ways, especially soil properties. Invasive species also alter the patterns of energy flow in trophic level interactions, food chains and food webs. Invasive species are well-known to modify the physical habitat as well as soil properties such as surface soil temperatures and hydrological processes, intensifying the disturbance regimes including flood, soil erosion and forest fires. By influencing the abiotic and biotic properties of the soil, invasive plants alter the soil's ability to support the same individuals or other individuals of the same invader species or other plant species and such interactions are known as 'plant-soil feedbacks', which play a crucial role in invasiveness (Lone et al. 2019).

A secondary forest is a forest that grows and develops naturally after damage or disturbance occurs in the climax forest. The secondary forest has a very strategic role in recovering a stable ecosystem as the primary forest (climax), ensuring the sustainability of environmental services and biodiversity in the long term. The entry of invasive plant species will disrupt and hinder the natural succession process. The formation of the climax forest becomes very slow and even natural succession fails, resulting in the loss of primary forest. There is not much information on the disturbance of weeds to secondary forest communities.

One of the invasive species not yet on the IUCN list but reported separately by Dillis et al. (2017) as invasive in Indonesia is *Bellucia pentamera*. This species came from the country of Costa Rica, Central America, which was introduced to Indonesia in the early 20th century through the Bogor Botanical Gardens. *B. pentamera* is a pioneer of small tree species with fast growth, able to quickly attack forest crevices, both those formed by fallen trees and logging, and able to reconstruct forest structure and create a monodominant canopy (Dillis et al. 2017). This ability is supported by its high biological reproduction in which one mature tree can produce thousands of fruits with thousands of fine seeds in each fruit. The fruit is fleshy and is eaten by various animals such as bats, birds, primates, insects, tapirs, turtles, ants, and humans (Dillis et al. 2018; Renner 1986). Currently, *B. pentamera* has spread in many places in Indonesia (Briggs et al. 2012; De Kok et al. 2015; Dillis et al. 2017; Dillis et al. 2018; Junaedi 2014; Kudo et al. 2014; Lindsell et al. 2015).

As an invasive plant, *B. pentamera* may benefit more from a changing climate because they have the potential to respond to shifting niches more rapidly than native plants. The impact of *B. pentamera* invasive plant disturbance on local plant species diversity, vegetation structure, and microclimate is still unknown. Many previous studies were limited to the response of *B. pentamera* to forest gaps and the presence of *B. pentamera* in disturbed habitats (Dillis et al. 2017; Dillis et al. 2018). Therefore, to expand the existing knowledge, this study aimed to investigate the impact of *B. pentamera* on species diversity, vegetation structure, and microclimate and soil conditions of secondary tropical forests.

MATERIALS AND METHODS

Study area and period

This study was conducted in Bukit Tengah Pulau forest, South Solok District, West Sumatra Province, Indonesia from March to June 2019. It is an isolated forest area within a landscape of oil palm plantation managed by PT. Kencana Sawit Indonesia (PT. KSI). Bukit Tengah Pulau forest is designated as a High Conservation Value Forest (HCVF) by PT. KSI with approximately 981 hectares or 9.6% of the total concession area. The HCVF is intended for the protection of local biodiversity and also as a source of water (Handru and Herwina 2012). The forest consists of old secondary forests and young secondary forests. The old secondary forest is characterized by a tree canopy with a height of more than 16 meters and 78% canopy cover, while the young one is dominated by local pioneer species and invasive species such as *B. pentamera*. The average rainfall per year is 4200 mm. The study was carried out at three different locations, namely site 1 (1°27'52.13" N, 101°31'24.64" E), site 2 (1°28'9.34" N, 101°31'27.36" E), and site 3 (1°28'13.01" N, 101°31'30.22"E) (Figure 1).

Data collection

Data were collected at three sites using a plot measuring 40 x 50 meters. The selection of the observation site was conducted purposively based on the proportion of the number of *B. pentamera* trees with non-*B. pentamera* trees

with the following categories: Site 1: The population of *B. pentamera* trees was higher than other non-*B. pentamera* trees. At this site, the proportion of *B. pentamera* trees was about 60% of the total trees in the plot (68 individuals out of 114 total trees) (i). Site 2: The population of *B. pentamera* trees is lower than other trees. At site 2, there was about 16% of *B. pentamera* tree; 14 individuals out of 85 total trees in plot (ii). Site 3: There was no *B. pentamera* tree at the site (iii).

At each site, 20 subplots measuring 10x10 m each were made for tree data collection, including species name, individual's number, and Diameter Breast Height (DBH) ≥ 10 cm. Within the 10 x 10 m subplot, a 5 x 5 m subplot was made for the sapling category to collect data of vegetation with DBH between 2 and ≥ 10 cm, while seedlings and understorey were observed in 1 x 1 m plot within the 5 x 5 m plot. The name of tree species in each life stage (trees, saplings, understorey) was identified directly in the field with the help of botanists from the Herbarium (ANDA), Andalas University. For unknown species, samples were collected (leaves, bark, fruit, and flowers (if any) and identified in the ANDA Herbarium, Andalas University. In each plot at the three research sites, environmental factors were measured, including light intensity, temperature and soil pH, and soil samples were taken to analyze soil water content, as well as the content of N, P, K and C.

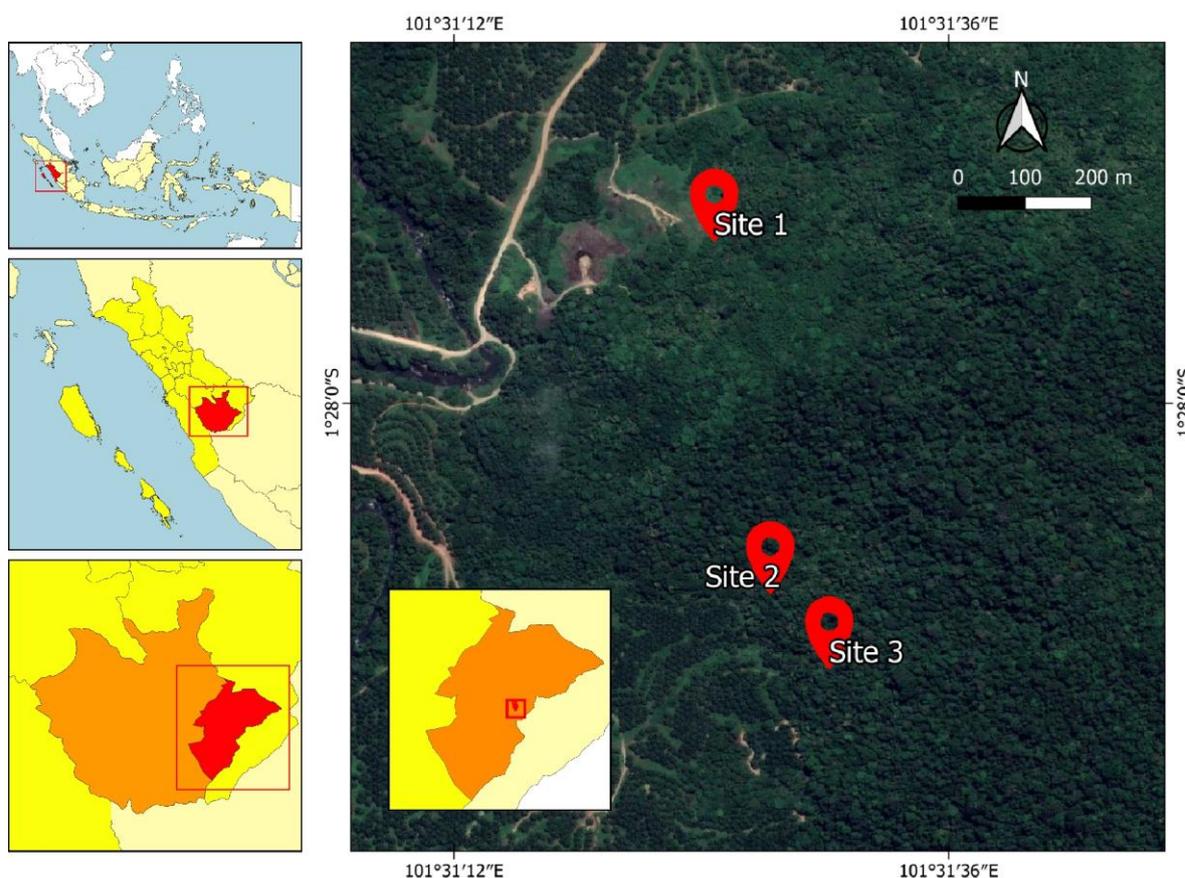


Figure 1. Map of study site in the Bukit Tengah Pulau forest, South Solok District, West Sumatra Province, Indonesia

Data analysis

The difference in the number of species, the Shannon-Wiener biodiversity index, and the Sorensen similarity index were analyzed using Microsoft Excel 2010. Species composition in plots, basal area, and Canonical Correlation Analysis was analyzed using PAST (Paleontological Statistics) software version 3:04 (Hammer 2014). Vegetation structure was calculated according to the formula of Mueller-Dombois and Ellenberg (1974) in the form of dominant species as follows:

Important Values Indeks (IVI): Relative Density (Rdi) + Relative Frequency (Rfi) + Relative Dominance (Rdo)

Where:

$$\text{Density} = \frac{\text{Number of a species}}{\text{Total area sampled}}$$

$$\text{Relative Density (Rdi)} = \frac{\text{Density of species}}{\text{Total density of all species}} \times 100\%$$

$$\text{Frequency} = \frac{\text{Total plots of a species occurs}}{\text{Total number of plots used}}$$

$$\text{Relative Frequency (Rfi)} = \frac{\text{Frequency of a species}}{\text{Total frequency of all species}} \times 100\%$$

$$\text{Dominance} = \frac{\text{Basal area a species}}{\text{Total area sampled}}$$

$$\text{Relative Dominance (Rdo)} = \frac{\text{Dominance of a species}}{\text{Total dominance of all species}} \times 100\%$$

RESULTS AND DISCUSSION

Species diversity and composition

The number of species and the tree diversity index, sapling and seedling decreased with the increase of *B. pentamera* trees. Site 1 (60% of *B. pentamera* trees) had the fewest number of species compared to site 2 (16% of *B. pentamera* trees) and site 3 (in the absence of *B. pentamera*). Species in the tree category were more diverse than sapling and seedling at all sites (Figure 2.A). The number of species was also reflected in the Shannon-

Wiener biodiversity index except for plot site 1, where the species in the sapling category were more diverse than tree species (Figure 2.B).

Based on Figure 2.A), it can be seen the number of species at the tree stage was 23, 46 and 74 species in site 1, site 2 and site 3, respectively. At the sapling level, there were 20, 31 and 58 species and at the understory level (including seedling) were 13, 16 and 36 species in site 1, site 2 and site 3, respectively. The observed plots in site 1 (60% of *B. pentamera* individuals) may not be able to show the full impact of *B. pentamera* on species diversity because local tree species fill the other 40%. Therefore, the species calculation was narrowed down to 16 selected subplots (1600 m²) composed of 86% of *B. pentamera* trees, while the other species only consisted of 10, 10 and 4 species for the category of tree, sapling and seedling/understorey vegetation, respectively. There were 5 species of understory vegetation in the category of shrub (*Clidemia hirta*), grasses (*Digitaria* sp.), and ferns (*Diplazium* sp., *Tectaria* sp., *Dicranopteris linearis*). In more detail, if we look at the eight subplots under the monodominant canopy of *B. pentamera* (100% of *B. pentamera* trees), only four saplings and one seedling were found.

This study demonstrated the negative effect of the invasive pioneer species *B. pentamera* on local tree species diversity. The presence of *B. pentamera* caused a decrease in the number of species and tree species diversity index. The higher the level of dominance of *B. pentamera*, the fewer plant species, and vice versa. This negative effect may be due to the ecological nature of *B. pentamera* with its ability to form a monodominant canopy (Dillis et al. 2017), thereby preventing other species from growing. *B. pentamera* plants with fast growth and a large number of fruits and seeds (Renner 1986) facilitate rapid colonization of a habitat, limiting resources and space for the growth of other species. This limiting factor has also been reported in other invasive species, such as *Prunus serotina* Ehrh., *Quercus rubra* L., and *Robinia pseudoacacia* L. The presence of these invasive species results in low natural regeneration of local trees (Dyderski and Jagodziński 2020).

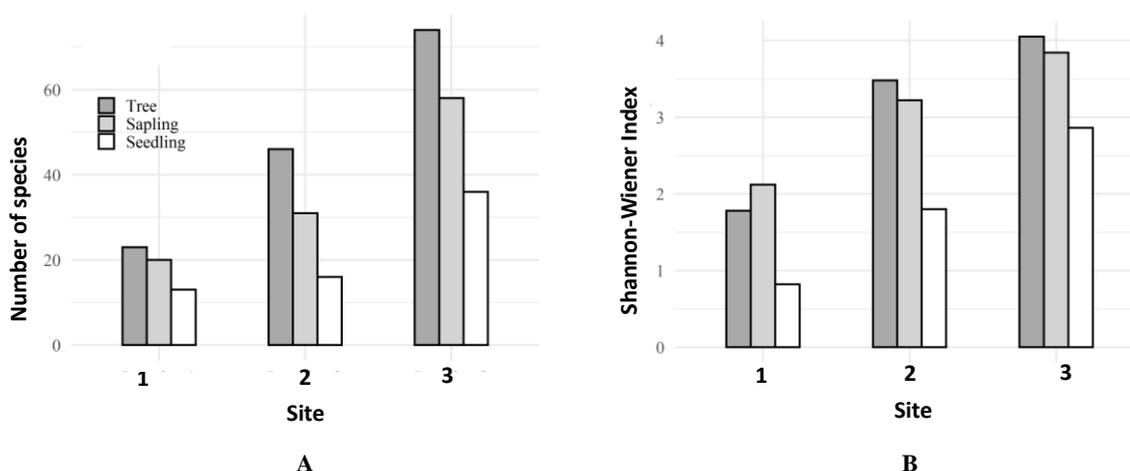


Figure 2. Differences in the number of species (A) and the Shannon-Wiener biodiversity index (B) of each life stage (tree, sapling, and seedling) in each of the study sites. Sites are differentiated according to the proportion between individuals of *B. pentamera* and non-*B. pentamera*

The diversity index value also decreased with the increasing density of *B. pentamera* (Figure 2B). The diversity index for the tree category was moderate at site 1 ($H' = 1.78$) and high at site 2 and 3 ($H' = 3.48$ and 4.05). Similarly, diversity index at the sapling level followed the pattern of the tree diversity index, which was moderate at site 1 ($H' = 2.12$) and high at sites 2 and 3 ($H' = 3.22$ and 3.84 respectively). For understorey, the diversity index was low at site 1 ($H' = 0.82$) and moderate at sites 2 and 3 ($H' = 1.8$ and 2.86 respectively). The result of this study is in accordance with the report of Powell et al. (2013) who compared heavily invaded and uninvaded sites in three biomes and concluded that plant communities invaded by non-native plant species generally have lower local richness.

The number of species at the tree level showed a significant difference between site 1 (60% of *B. pentamera* trees) and site 3 (no individual *B. pentamera*) with p -value = 0.03. The number of saplings species also showed significant differences at site 1 and site 3 (p -value = 0.0005) as well as site 2 and site 3 with a p -value 0.0007 (Figure 3). In contrast to the number of understorey species, which did not show significant differences between sites (p -value > 0.05).

The similarity index between sites in the tree, sapling, and understorey categories had various values and was relatively low (less than 50%) (Figure 4). Mueller-Dombois and Ellenberg (1974) state that the similarity index is considered significant if its value is more than 50%. The similarity index for the tree, sapling, and understorey levels tended to be higher between site 2 and site 1, with the highest similarity value being the understorey category, which is 20.68%. The lowest similarity index value was found for the sapling level between site 2 and site 3, which was 2.24% (Figure 4).

Vegetation structure

The vegetation structure is reflected by the value of density, frequency, the dominance of the basal area value, and important value index (IVI) of each species. Table 1 presents the top ten species in the tree, sapling, and

seedling/understorey categories based on the highest IVI at each study site. The vegetation at site 1 was composed of 23 species with 114 tree individuals in a 2000 m² area, of which 68 individuals (60%) were *B. pentamera* species. This species was almost evenly distributed within the plots which were found in 19 of the 20 subplots. The relative dominance based on the calculation of the basal area of this invasive species was 38%, making it the most dominant species compared to other species with an IVI of 130%. Other dominant species that made up the vegetation structure were *Croton argyratus*, *Ficus variegata*, *Endospermum diadenum*, *Callicarpa acuminata* and *Archidendron ellipticum*, while other species had IVI of less than 10% (Table 1). These species dominated the vegetation with different vegetation structure parameters. Some species dominated in terms of the number of individuals (density) and some dominated in terms of the basal area (dominance).

Sapling category was also dominated by *B. pentamera*, which were distributed in 12 of the 20 sub-plots of observation. With a plot area of a quarter of the tree measurement plot, the number of saplings of *B. pentamera* was half of the number of trees, meaning that the number of saplings of *B. pentamera* was twice the number of trees in the community. Similar to the tree level, *C. argyratus* was also one of the dominant species at the sapling level, followed by *Swintonia floribunda*, *Glochidion acuminatum*, *Vitex vestita*, *Polyalthia spathulata*, *F. variegata* and *Ficus globosa*. In contrast to trees, the order of dominance of the species at the sapling stage was characterized by the values of the three structural parameters which were also sequential. The understorey vegetation was not dominated by seedling from tree group, but from the shrub group *C. hirta*, with a total of 295 individuals spread over 16 sub-plots, while seedling from the tree group was still dominated by *B. pentamera* and *C. argyratus*. Despite the fact that *B. pentamera* was the dominant species in this site, two Dipterocarpaceae species, *Parashorea densiflora* and *Parashorea lucida*, were recorded. These two species are not included in Table 1 because the important value index is small and they are not among the ten main species in site 1.

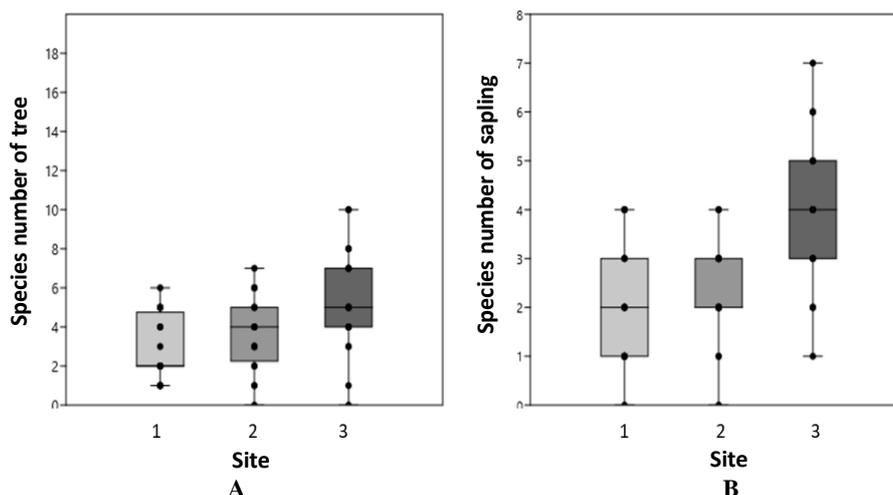


Figure 3. Analysis of the difference in the species number of tree (A) and sapling (B) among sites

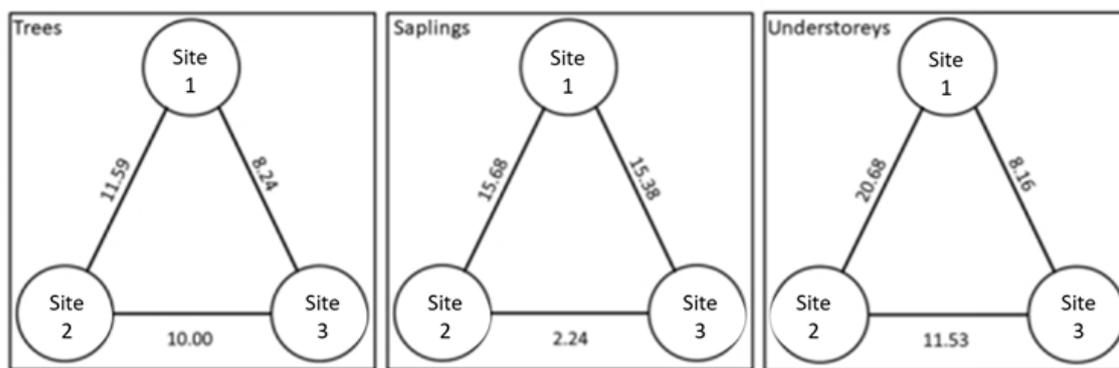


Figure 4. Sorensen Similarity Index (%) of trees, saplings and understorey between the three sites

At site 2, *B. pentamera* shared space with 45 other tree species but still dominated the vegetation with IVI of 33.68%, while the other six dominant species were local climax tree species. *B. pentamera* dominated the vegetation with a total of 14 individuals spread over seven of the 20 sub-plots with a dominant basal area of 8%. Two other dominant species, namely *Lepisanthes* sp. and *Shorea palviflora*, dominated the plot area with a basal area similar to *B. pentamera*. Sapling was dominated by *B. pentamera* with IVI of 32.86%, almost the same as the tree category, making it have the highest relative density and frequency compared to other species. Still, it had a smaller basal area dominance than *Blumeodendron* sp. It was the second dominant species after *B. pentamera*, followed by *Aporosa* sp. and *Parashorea lucida*. The understorey was not dominated by seedling of tree vegetation but by *C. hirta* shrub and *Selaginella willdenowii*. However, *B. pentamera* and *C. argyratus* were still found as the two dominant seedling species on the forest floor. Besides being dominant in the tree category, *B. pentamera* was also prevalent in the sapling category. This condition explains the fast growth rate of *B. pentamera* both vertically and horizontally compared to other species. It can be a limiting factor for local species to grow and thrive among the densely packed *B. pentamera* individuals.

The site 3 (none of *B. pentamera*) was composed of various climax tree species such as *Palaquium warsurifolium*, *Quercus argentata*, and *Shorea leprosula*. However, two of the three most dominant species at this site were local pioneer species (*C. argyratus* and *Macaranga hypoleuca*), and late pioneer species, *E. diadenum* with IVI of 8.3%. The species with the highest IVI was *Palaquium warsurifolium* (21.15%). This value indicates that no single species dominated the area but shared space with many other species. The dominant sapling was a pioneer species *C. argyratus* with an IVI of 25.81%, which dominated the vegetation on the forest floor, followed by local climax species such as *Parashorea*

lucida (IVI = 14.78%) as the representative of the top canopy species. Besides local tree saplings, undergrowth at site 3 was also composed of shrub species *C. hirta* and *Melastoma malabathricum* as well as *Selaginella*.

Based on Table 1, differences in *B. pentamera* dominance between site 1 and site 2 indicated differences in the intensity of vegetation disturbance between the two sites. Site 1 was more disturbed than site 2, providing more room for growth and development of *B. pentamera* with low competition from other species. Lozon and MacIsaac (1997) stated that invasive species develop in degraded forests; therefore, the higher of vegetation being disturbed, the greater the dominance of an invasive species. This statement is linear with the findings of Dillis et al. (2017) that indicates *B. pentamera* is more commonly found in canopy gaps formed by selective logging than canopy gaps created naturally by fallen trees. The fallen trees in disturbed vegetation initiate the development of *B. pentamera* higher than fallen trees in primary forest. Therefore, the intensity of vegetation disturbance determines the invasiveness of *B. pentamera* and its effect on the development of local species. High disturbances will encourage the dominance of *B. pentamera* and become a barrier for local vegetation to develop. Vice versa, the high occurrence of local plant diversity might hinder *B. pentamera* from thriving. Site 3 had the highest species diversity than sites 1 and 2, although it is lower than that of post-logged forest in Hutan Harapan, where 81 species of sapling and seedling were found in 160 m² (Kardiman 2019). Although not invaded by *B. pentamera*, site 3 had also been disturbed, which was indicated by the presence of some local pioneer tree species such as *C. argyratus* and *M. hypoleuca*. The presence of pioneer species and invasive species is an indication of vegetation disturbance (Goodale et al. 2012; Lozon and MacIsaac 1997). The absence of *B. pentamera* in site 3 could be attributed to the earlier development of the local pioneer species, constraining the development of *B. pentamera*.

Table 1. Relatif Density (RDi), Relatif Frequency (RFi), Relatif Dominance (RDo) and Important Value Index (IVI) of the ten most important species of each vegetation category across three sites

Species	Family	Rdi (%)	Rfi (%)	Rdo (%)	IVI (%)
Site 1 (60 % population of <i>B. pentamera</i>)					
Tree					
<i>Bellucia pentamera</i> Naudin	Melastomataceae	59.65	33.33	37.82	130.80
<i>Croton argyratus</i> Blume	Euphorbiaceae	8.77	12.28	6.58	27.63
<i>Ficus variegata</i> Blume	Moraceae	3.51	7.02	15.94	26.47
<i>Endospermum diadenum</i> (Miq.) Airy Shaw	Euphorbiaceae	3.51	5.26	8.13	16.91
<i>Callicarpa acuminata</i> Kunth	Lamiaceae	4.39	5.26	6.12	15.77
<i>Archidendron ellipticum</i> (Blanco) I.C.Nielsen	Leguminosae	2.63	5.26	2.95	10.84
<i>Macaranga hypoleuca</i> (Rchb.f. & Zoll.) Müll.Arg.	Euphorbiaceae	1.75	3.51	3.18	8.44
<i>Dialium kunstleri</i> Prain	Leguminosae	1.75	1.75	3.18	6.68
<i>Quercus argentata</i> Korth.	Fagaceae	0.88	1.75	2.69	5.32
<i>Ficus aurata</i> (Miq).	Moraceae	0.88	1.75	2.59	5.22
Sapling					
<i>Bellucia pentamera</i> Naudin	Melastomataceae	45.71	27.27	29.84	102.83
<i>Croton argyratus</i> Blume	Euphorbiaceae	12.86	11.36	11.14	35.36
<i>Swintonia floribunda</i> Griff.	Anacardiaceae	4.29	6.82	11.02	22.13
<i>Glochidion acuminatum</i> Müll.Arg	Phyllanthaceae	2.86	4.55	9.58	16.98
<i>Vitex vestita</i> Müll.Arg	Lamiaceae	5.71	4.55	6.46	16.72
<i>Polyathia spathulata</i> Boerl	Annonaceae	4.29	6.82	3.45	14.56
<i>Ficus variegata</i> Blume	Moraceae	2.86	4.55	5.46	12.86
<i>Ficus globosa</i> Blume	Moraceae	1.43	2.27	6.46	10.16
<i>Syzygium scortechinii</i> (King) Chantaran.& J.Par	Myrtaceae	2.86	4.55	1.78	9.18
<i>Archidendron ellipticum</i> (Blanco) I.C.Nielsen	Leguminosae	1.43	2.27	1.89	5.59
Understorey					
<i>Clidemia hirta</i> (L.) D.Don	Melastomataceae	80.60	35.56	-	116.16
<i>Bellucia pentamera</i> Naudin	Melastomataceae	6.56	17.78	-	24.34
<i>Croton argyratus</i> Blume	Euphorbiaceae	6.01	17.78	-	23.79
<i>Digitaria</i> sp.	Graminae	2.73	6.67	-	9.40
<i>Tectaria</i> sp.	Tectariaceae	0.55	4.44	-	4.99
<i>Ficus aurata</i> (Miq).	Moraceae	1.64	2.22	-	3.86
<i>Ficus variegata</i> Blume	Moraceae	0.27	2.22	-	2.50
<i>Sapium</i> sp.	Euphorbiaceae	0.27	2.22	-	2.50
<i>Aglaiia argentea</i> Blume	Meliaceae	0.27	2.22	-	2.50
<i>Horsfieldia punctatifolia</i> J.Sinclair	Myristicaceae	0.27	2.22	-	2.50
Site 2 (16 % population of <i>B. pentamera</i>)					
Tree					
<i>Bellucia pentamera</i> Naudin	Melastomataceae	16.47	9.21	8.00	33.68
<i>Lepisanthes</i> sp.	Sapindaceae	5.88	6.58	7.55	20.01
<i>Syzygium</i> sp.	Myrtaceae	3.53	3.95	6.96	14.44
<i>Callicarpa arborea</i> Roxb.	Lamiaceae	4.71	2.63	5.42	12.76
<i>Shorea parvifolia</i> Dyer	Dipterocarpaceae	2.35	2.63	7.75	12.73
<i>Quercus argentata</i> Korth.	Fagaceae	3.53	3.95	4.97	12.45
<i>Parashorea lucida</i> Kurz	Dipterocarpaceae	4.71	5.26	2.30	12.27
<i>Popowia pisocarpa</i> (Blume) Endl.exWalp.	Anonaceae	3.53	3.95	4.59	12.07
<i>Croton argyratus</i> Blume	Euphorbiaceae	4.71	5.26	1.59	11.56
<i>Syzygium antisepticum</i> (Blume) Merr.&L.M.Perry	Myrtaceae	2.35	2.63	5.60	10.58
Sapling					
<i>Bellucia pentamera</i> Naudin	Melastomataceae	11.76	11.11	9.99	32.86
<i>Blumeodendron</i> sp.	Euphorbiaceae	7.84	2.22	12.42	22.49
<i>Aporosa</i> sp.	Phyllanthaceae	7.84	8.89	5.24	21.97
<i>Parashorea lucida</i> Kurz	Dipterocarpaceae	5.88	6.67	7.67	20.22
<i>Croton argyratus</i> Blume	Euphorbiaceae	7.84	6.67	4.26	18.77
<i>Popowia pisocarpa</i> (Blume) Endl.exWalp.	Annonaceae	3.92	4.44	7.67	16.04
<i>Callicarpa arborea</i> Roxb.	Lamiaceae	3.92	2.22	7.55	13.70
<i>Pimelodendron griffithianum</i> (Müll.Arg.) Benth. Ex.Hook f	Euphorbiaceae	3.92	4.44	2.19	10.56
<i>Tabernaemontana</i> sp.	Euphorbiaceae	3.92	4.44	1.95	10.31
<i>Sindora wallichii</i> Bent	Leguminoceae	1.96	2.22	5.60	9.79

Understorey

<i>Clidemia hirta</i> (L.)D.Don	Melastomataceae	50.41	25.53	-	75.94
<i>Selaginella willdenowii</i> (Desv. exPoir.) Baker	Selaginellaceae	18.70	14.89	-	33.59
<i>Popowia pisocarpa</i> (Blume) Endl.exWalp	Annonaceae	4.88	12.77	-	17.64
<i>Croton argyratus</i> Blume	Euphorbiaceae	4.88	10.64	-	15.52
<i>Bellucia pentamera</i> Naudin	Melastomataceae	6.50	8.51	-	15.01
<i>Lasianthus tomentosus</i> Blume	Rubiaceae	4.07	6.38	-	10.45
<i>Lantana camara</i> L.	Verbenaceae	2.44	2.13	-	4.57
<i>Borreria laevis</i> (Lam.) Griseb.	Rubiaceae	1.63	2.13	-	3.75
<i>Knema laurina</i> Warb.	Myristicaceae	0.81	2.13	-	2.94
<i>Symplocos</i> sp.	Symplocaceae	0.81	2.13	-	2.94

Site 3 (None of *B. pentamera*)**Tree**

<i>Palaquium warsurifolium</i> Pierre exDubard.	Sapotaceae	7.77	8.00	5.38	21.15
<i>Croton argyratus</i> Blume	Euphorbiaceae	8.74	8.00	3.29	20.02
<i>Macaranga hypoleuca</i> (Reichb.f &Zoll)	Euphorbiaceae	4.85	4.00	4.35	13.21
<i>Quercus argentata</i> Korth.,	Fagaceae	0.97	1.00	7.19	9.17
<i>Madhuca sericea</i> H.JLam	Sapotaceae	1.94	2.00	4.67	8.61
<i>Endospermum diadenum</i> (Miq.) AiryShaw	Euphorbiaceae	0.97	1.00	6.30	8.27
<i>Lepisanthes</i> sp.	Sapindaceae	1.94	2.00	2.80	6.74
<i>Shorea leprosula</i> miq	Dipterocarpaceae	1.94	2.00	2.48	6.42
<i>Melicope</i> sp.	Rutaceae	2.91	1.00	1.79	5.70
<i>Cryptocarya</i> sp.	Lauraceae	1.94	2.00	1.75	5.69

Sapling

<i>Croton argyratus</i> Blume	Euphorbiaceae	9.41	6.17	10.22	25.81
<i>Parashorea lucida</i> Kurz	Dipterocarpaceae	5.88	6.17	2.72	14.78
<i>Syzigium racemosum</i> Blume	Myrtaceae	1.18	1.23	7.50	9.91
<i>Gynotroches axillaris</i> Blume	Rhizophoraceae	3.53	2.47	3.70	9.70
<i>Baccaurea parviflora</i> (Mull Arg)	Euphorbiaceae	3.53	3.70	1.88	9.12
<i>Syzigium scorthechinii</i> (King) Chantar. & J. Parn.	Myrtaceae	4.71	2.47	1.75	8.93
<i>Cinamomum inners</i> Reinw. Ex Bl	Lauraceae	3.53	2.47	2.81	8.81
<i>Dacryodes rugosa</i> (Bl.)H.J.Lam	Burseraceae	3.53	3.70	1.40	8.64
<i>Horsefeldia pallidiacaula</i> WJdeWilde	Myristicaceae	3.53	3.70	1.20	8.43
<i>Knema laurina</i> (Blume)Warb.	Myristicaceae	1.18	1.23	5.73	8.14

Understorey

<i>Croton argyratus</i> Blume	Euphorbiaceae	25.44	12.50	-	37.94
<i>Clidemia hirta</i> (L.) D.Don	Melastomataceae	15.79	12.50	-	28.29
<i>Selaginella</i> sp.	Selaginellaceae	7.89	6.25	-	14.14
<i>Coffea robusta</i> L.Linden	Rubiaceae	4.39	2.08	-	6.47
<i>Tinospora cordifolia</i> (Wild) Hook. F. and Thoms (Guduchi)	Menispermaceae	4.39	2.08	-	6.47
<i>Syzigium</i> sp.	Myrtaceae	3.51	2.08	-	5.59
<i>Polyalthia</i> sp.	Annonaceae	3.51	2.08	-	5.59
<i>Melastoma malabatricum</i> L.	Melastomataceae	3.51	2.08	-	5.59
<i>Archidendron ellipticum</i> (Blume) I.C.Nielsen	Leguminosae	3.51	2.08	-	4.71
<i>Achyranthes mutica</i> A. Grey ex H.Mann	Rubiaceae	1.75	2.08	-	3.84

Although the invasion of *B. pentamera* resulted in a decrease in plant species diversity at site 1 and site 2, there were still top canopy climax tree species usually found in the primary dipterocarp forest. In both sites, selective logging activities had caused vegetation damage, and local tree species in the sapling and seedling category were the remnants of logging that grew after or concurrently with *B. pentamera*. Species from the family Dipterocarpaceae are the main characteristics of primary forests in tropical Southeast Asia, forming upper canopy strata to emergent ones (Laumonier 1997). Most of these primary forest plant species were found at site 3, which was not invaded by *B. pentamera*. The existence of such climax species might

serve as a genetic resource for vegetation regeneration to form a complete stand structure. Although the number of climax species at site 1 was less than at site 3, this study revealed that *B. pentamera* did not completely inhibit local species from growing. Therefore, the composition of climax species will naturally continue to increase, both from the parent trees remaining in the plot and through seed dispersals either by wind or animals. Nonetheless, since light intensity reaching the forest floor on-site was high, it might cause vegetation regeneration to be dominated by *B. pentamera* for a long time unless intervention is carried out with restoration.

Site 3 was dominated by three plant species and two of them were pioneer species. This indicates that this site was also disturbed or referred to as a secondary forest. These pioneer species are usually found in young and old secondary forests (Laumonier 1997). Furthermore, Laumonier (1997) reported that young secondary forest was dominated by trees with a height of 5-15 m. Since site 3 had vegetation with a tree height of more than 20 m, thus it can be classified as an old secondary forest. Briggs et al. (2012) reported that *B. pentamera* became the dominant species together with *M. gigantea* in young and mid secondary forests in Hutan Harapan, Jambi. In three studied sites, the shrub species *C. hirta* was found on the forest floor. This species grows well in tropical climates and can occur in disturbed and undisturbed habitats.

The intensity of vegetation disturbance which was followed by the invasion of *B. pentamera* formed a new vegetation structure. Three important parameters (density, distribution, and basal area) describe how each species occupies space in the forest structure. As an invasive species, *B. pentamera* quickly fills the open canopy gap caused by forest disturbance (Dillis et al. 2017). This can be seen from a large number of individuals and their even distribution in the plot. However, in terms of basal area (dominance), this species was small when compared to the third dominant species, namely *F. variegata*. Despite *B. pentamera* was 17 times more abundant than *F. variegata*, but the basal area was only 2.5 times larger than *F. variegata*, meaning that *F. variegata* had few individuals but with large stem size and canopy cover. A similar condition was also found between *C. argyrateus* and *E. diadenum*. Vegetation regeneration occurs naturally, where species that are dominant at the tree level are also dominant at the sapling and seedling levels. Despite the presence of *C. hirta* shrub, it did not inhibit tree saplings from growing (Kardiman et al. 2019). At site 2, *B. pentamera* also showed the same phenomena where *B. pentamera* dominated with 7 individuals (RD_i = 16.47% and RF_i = 9.21%) with a relatively small size (RDo = 8%) almost the same as the basal area of the local climax type, *Shorea parviflora* with a total individual of 2 (RD_i = 2.35%; RF_i =

2.63% and (RDo = 7.75%). In Figure 5, it can be seen that the more dominant *B. pentamera* is, the smaller the basal area of the tree.

The density of *B. pentamera* at a site affected the basal area at tree and sapling levels, as shown in Figure 5. The basal area of tree-level vegetation at site 1 showed a significant difference with site 3 (p-value = 0.013). The basal area of the tree at site 2 also showed a significant difference with site 3 with p value = 0.005. This condition indicates that the more dominant *B. pentamera* is, the lower the level of dominance of local species.

Effect of *B. pentamera* on microclimate and soil

The presence of *B. pentamera* affected microclimate and soil conditions as presented in Table 4 which shows the measurements of soil water content, soil pH, air temperature, relative light intensity, and soil nutrient content (N, P, K, C).

Site 1 had a soil moisture content of about 2% lower than that of site 3. In other words, the soil became drier as the dominance of *B. pentamera* increased. Furthermore, there was no difference in soil pH, while air temperature and light intensity were higher at the site invaded by *B. pentamera* (Table 2). Nonetheless, *B. pentamera* had a positive effect on soil nutrients, especially for elements of Nitrogen (N) and Phosphorus (P), where their percentage was higher than soil in site 3. The elements Kalium (K) and Carbon (C) were lower at site 2.

The lower soil water content at site 1 could be a limiting factor for local species to compete with the invasive species. According to Pfeiffer and Gorchov (2015), weed species have a strong root ability to absorb large amounts of groundwater. This is in line with the character of *B. pentamera* whose life form is a tree in which this species can grow faster than local pioneer species (Dillis 2017) and grow taller than the local climax species. Arx (2013) explains that forest ecosystems have a distinct below-canopy microclimate which is regulated by diverse biophysical processes, and of eminent importance to the growth and survival of understory vegetation and seedlings.

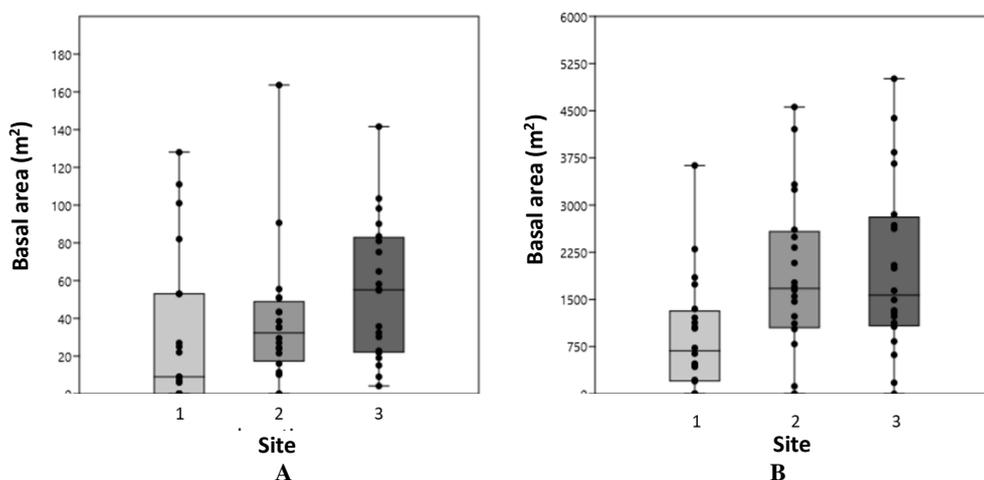


Figure 5. Basal area of tree (A) and sapling (B) across three studied sites

Changes in vegetation structure can affect soil and air temperature, as happened at the study site. The vegetation invaded by *B. pentamera* had drier soil and higher temperatures due to the high intensity of sunlight on the vegetation floor. However, *B. pentamera* with a monodominant canopy can protect the forest floor from direct light penetration. The microclimate at site 1 may be better than that in open areas without vegetation. The site where *B. pentamera* absence was not a primary forest without disturbance, but still the microclimate was better than the sites where *B. pentamera* was present. However, *B. pentamera* improved soil conditions in term of nitrogen and phosphorus, but not much different for potassium and soil carbon. In this case, the invasive species *B. pentamera* had the same effect as the invasive species in general in which they can improve the nutrients of barren soil (Dassonville et al. 2008). The N content of the soil at site 1 was higher than at the other two sites. Jo et al. (2017) stated that invasive plants increase the N cycle by increasing the flow of N to the soil through greater litter production. Litter decomposition is an important step in the nutrient cycle and can provide nutrients to plants. Each ecosystem has certain physical and environmental conditions that cause differences

in species composition. Each type of tree affects the rate of decomposition of litter differently because the quality of the litter is different and is closely related to soil microbial communities and soil nutrient cycles (Devianti et al. 2017). The high level of soil nutrients is undoubtedly perfect for the invasive species itself and the local climax species that grow together in the community. The development of these plant communities could be better because invasive species can also increase the intensity of soil mycorrhizal fungi (Meinhardt and Gehring 2012).

The canonical correlation analysis between abiotic factors and dominant tree species explains the variation in abiotic conditions and their relationship to the species that dominated each research site as shown in Figure 6. Site 1 was characterized by high temperature and positively correlated with light intensity, thus this site had low soil water, and vice versa. Species diversity also shows a relationship with environmental factors, where high soil water content was positively related to plant species diversity, especially tree stands. Understorey did not vary in high light, while forest floor temperatures were high in areas with low tree species variation, and vice versa.

Table 2. Microclimate and soil nutrients across the three studied site

Plot site	Soil water (%)	Soil pH	Temperature (°C)	Relative light intensity (%)	N (%)	P (%)	K (%)	C (%)
Site 1	23.4	7	29.3	18.25	4.41	0.497	0.824	16.35
Site 2	24.7	7	28.6	18.06	4.05	0.457	0.703	13.128
Site 3	25.1	7	28.3	15.88	3.01	0.353	0.831	17.177

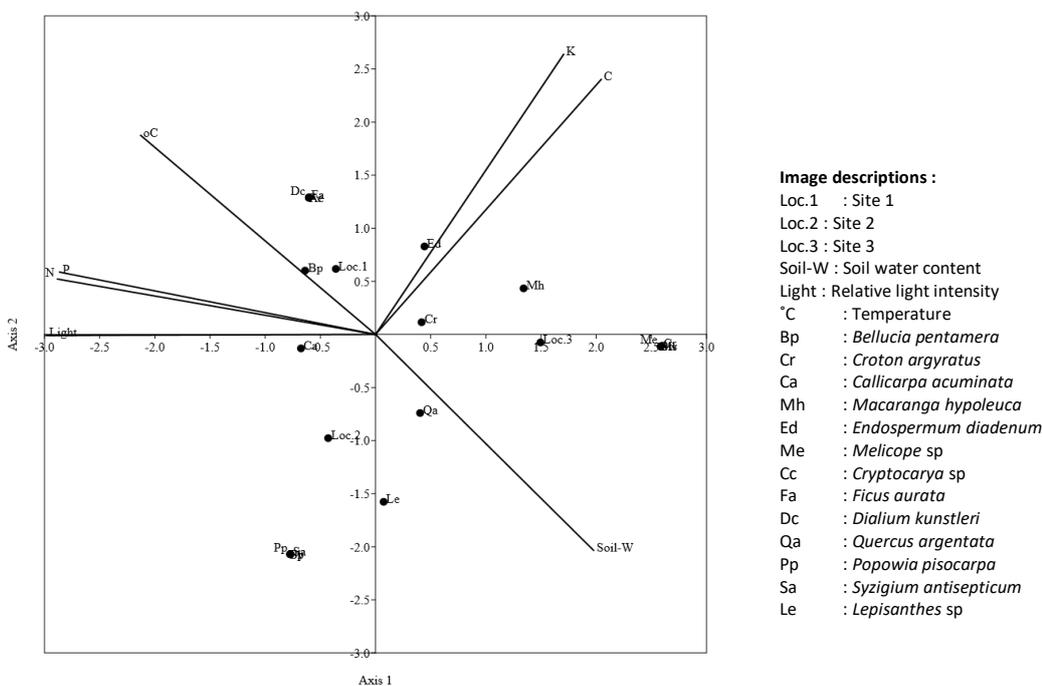


Figure 6. Canonical Correlation Analysis (CCA) of abiotic factors and dominant tree species in the three study sites

It can be concluded that the invasion of *B. pentamera* affected plant diversity, microclimate and soil in secondary forests. Species diversity decreased with the increase in the dominance of *B. pentamera*. The site that was not invaded by *B. pentamera* was composed of several climax species ranging from tree, sapling and seedling levels. The secondary forest of Bukit Tengah Pulau can be divided into two categories, namely young secondary forest dominated by the invasive plant *B. pentamera*, and the old secondary forest dominated by local pioneer tree species. Both types of secondary forests had to regenerate stock of climax type. The presence of *B. pentamera* deteriorated the microclimate of the secondary forest, but it had a positive impact on the nitrogen and phosphorus contents of the soil.

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