

Review Article

Some Abiotic and Biotic Factors Influencing Firefly Population Abundance in Southeast Asia: A Review

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ABSTRACT

This paper reviews biotic and abiotic factors that influence the life cycle of fireflies. This review paper has screened and chosen articles by using Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) from two databases: Semantic Scholar (n = 1080) and Google Scholar (n = 2280). From this review, generally, abiotic factors, i.e., water level in soil, air temperature, air humidity, rainy season, altitude, water salinity (NaCl), wind direction, wind speed, dissolved oxygen (DO), biochemical oxygen demand (BOD), chemical oxygen demand (COD), ammonia nitrogen (NH₃-N) and maximum air pollution index (API) were most likely influenced the population abundance and distribution of the fireflies in Southeast Asia. Biotic factors include the presence of *Cyclotropis carinata* snails, vegetation health, tree suitability (leaf size, density, arrangement of leaves, tree location), insecticides (Saponins) in some vegetation species, plant structural architecture, and food (nectar and sap) were the most likely to influence the presence of fireflies species even though synchronous firefly of Southeast Asia were found in other vegetation species, *Sonneratia caseolaris* (Berembang) still the most preferred display tree. From this

review, we also found that Malaysia has the highest reported findings on firefly studies in this region. To conclude, numerous abiotic and biotic elements should be researched further to determine their relationship to firefly populations and other vertebrate - invertebrates in their natural environment.

Keywords: Abiotic, biotic, fireflies, mangrove, Southeast Asia

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INTRODUCTION

There are generally various species of fireflies that can be found in all parts of the world. They are mainly distributed in the tropical areas of Southeast Asia (Branham, 2002), with eleven species of the *Pteroptyx* genus identified in Southeast Asia (Ballantyne, 2001). Terrestrial arthropods, insects, and beetle species may be found worldwide in a wide range of biogeographical locations (Table 1). It is estimated that around 15% of insect species are in the north temperate region, while the remainder lives in the tropics and south temperate regions. The neotropics may have more than 1.6 million insect species, with comparable counts for the Australasian and Indo-Malayan areas combined and fewer than a million species for the Afrotropical region (Table 1) (Stork, 2018). Insect species are likely to experience a variety of conditions as they spread across different biogeographical regions. Because abiotic factors are variable in different climates, these species will have distinct abiotic factor requirements. There are around 5.5 million insects, 1.5 million beetles, and 7 million terrestrial arthropods species known worldwide (Stork, 2018), with about 2000 known species of fireflies (Coleoptera: Lampyridae) all around the globe (Lewis et al. 2020). The Lampyridae consists of non-luminous adults, flightless female fireflies, and lightning insects (Lewis et al., 2020). According to Matalin and Wiesner (2006), Latreille (1817) established and defined fireflies as insects belonging to the family Lampyridae of the Coleoptera order. Since then, many new species have been described, and some significant range extensions have been reported. In addition, fireflies can be found in temperate to tropical regions (Chan, 2012).

Thailand, Malaysia, Cambodia, Indonesia, the Philippines, New Guinea, and Sulawesi are among the tropical climate countries where fireflies are extensively spread, and various firefly species exist (Ballantyne & McLean, 1970; Ballantyne & Lambkin, 2001; Nuranca et al., 2013; Jusoh et al., 2018; Sartsanga et al., 2018). In Southeast Asia and the Indo-Pacific region, over 400 species have been identified, most of which are members of the Luciolinae family (Ballantyne et al., 2015). Seri and Rahman (2021) successfully identified 145 firefly species across Southeast Asian countries (including Malaysia, the Philippines, Indonesia, Cambodia, Myanmar, Singapore, Sri Lanka, Papua New Guinea, Laos, Thailand, and Vietnam). At the same time, the authors were also unsuccessful in locating studies in Brunei. Additionally, they noted that data on firefly species found in countries such as the Philippines, Indonesia, Cambodia, Myanmar, Singapore, Sri Lanka, Papua New Guinea, Laos, and Vietnam is extremely outdated due to the country's lack of research (Seri & Rahman, 2021). Regretfully, there has been a decline in the distribution and abundance of numerous firefly species during the previous few decades (Lauff, 2017; Lloyd, 2018). However, since 2007, the firefly population in Kampung Kuantan, Kuala Selangor, Selangor has decreased by 42% in ten years as a result of riverbank cleaning (Nadirah et al., 2020).

Table 1

Estimated numbers of terrestrial arthropods, insects, and beetle species in various biogeographic areas (Stork, 2018)

Region	Number of arthropod species	Number of insect species	Number of beetle species
Australasia	890,799	720,521	196,515
Afrotropical	1,205,639	975,179	265,971
Central America	760,240	614,918	167,713
Indo-Malayan	908,479	734,822	200,416
North America	142,800	115,503	31,502
Neotropics	2,003,279	1,620,348	441,935
Oceanic	240,720	194,706	53,104
Palaearctic	648,040	524,165	142,961
Total	648,040	5,500,163	1,500,118

Fireflies produce synchronized spectacle light when congregating in colonies on certain trees. They are commonly seen on Berembang trees (*Sonneratia caseolaris*) (Nada & Kirton, 2004). The most well-known genus due to its spectacular synchronized flashing is *Pteroptyx* fireflies. They are native to coastal areas and riverbanks in Southeast Asia (McKenna & Farrell, 2009). Various techniques have been used to monitor changes in the abundance of *Pteroptyx* species in particular locations, such as the use of land-use spatial analysis of satellite images (Jusoh et al., 2009; Jusoh et al., 2012); non-destructive estimation methods (i.e., a percentage cover chart based on firefly flashing; visual method) (Jusoh et al., 2010a; Shahara et al., 2017); visual counting methods (Prasertkul, 2018); and digital night photography and image analysis digital night photography of the vegetation (non-destructive method) (Khoo et al., 2012). Meanwhile, several studies examining the habitat requirements of fireflies and the factors affecting their abundance have been conducted using a variety of techniques, including photo visual analysis using a high-resolution camera (720 pixels HD) (Faudzi et al., 2021); sweep-netting sampling (Abdullah et al., 2019; Hazmi & Sagaff, 2017); combination between visual counting and sweep net (Jaikla et al., 2020) and visual assessment and aerial net sampling (Foo & Mahadimenakbar, 2015). However, these studies have limitations and should be improved to understand better how specific factors affect the population abundance of these fireflies and their ecological requirements. For example, based on the findings of previous studies, many studies focus exclusively on the short adult phase life cycle of fireflies, although the most prolonged development period happens below the soil surface (especially the stage). Thus, this paper

review aims to evaluate experimental findings on the influence of various biotic and abiotic factors on firefly populations (Coleoptera: Lampyridae) throughout Southeast Asia.

METHODOLOGY

This study employed a systematic literature review; journal articles were sourced from two of the largest online databases: Semantic Scholar (n = 1080) and Google Scholar (n = 2280). Both review and empirical studies included in the literature review were from the reputable journals, primarily indexed by SCOPUS, and some by Web of Science, namely the *Biodiversity Data Journal*, *International Journal of Tropical Insect Science*, *Oriental Insects*, *Transactions of the American Entomological Society*, *Insects*, *Raffles Bulletin of Zoology*, *BioRisk*, *Sepilok Bulletin*, *Journal of Tropical Biology & Conservation*, *Ecology and General Biology*, *Royal Society Open Science*, *Journal of Asia-Pacific Biodiversity*, *Malaysian Applied Biology*, *Wetlands Ecology and Management*, *Lampyrid*, *Zootaxa*, *Environment and Natural Resources Journal*, *Chemosphere*, *BioScience*, *Journal of Insect Conservation*, *Biodiversity*, *Aquatic Botany*, *Modern Applied Science*, *Science Report of the Yokosuka City Museum*, *Journal of Natural Remedies*, *Pertanika Journal of Tropical Agricultural Science*, *The Coleopterists Bulletin*, *Journal of Insect Behavior*, *Malayan Nature Journal*, *Annual Review of Entomology* and *NU International Journal of Science*.

The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) technique was used to methodically pick relevant research from the available literature in this paper review writing. Four phases need to be followed using the PRISMA method: identification, screening, eligibility, and inclusion (Figure 1). Among the keywords used when searching journal articles from the database are: “Fireflies,” “Fireflies in Southeast Asia,” “Abiotic,” “Biotic,” “Mangrove,” “*Pteroptyx* fireflies,” “Life Cycle,” and “Water Quality.”

RESULTS AND DISCUSSION

According to previous studies, the most frequently employed approach was sweep-netting sampling, as in the study by Wattanachaiyingcharoen et al. (2011); Shahara et al. (2017); Jusoh et al. (2010a); Abdullah et al. (2019); Abdullah et al. (2020); Hazmi and Sagaff (2017); Badruddin and Ballantyne (2020); Sriboonlert et al. (2015) Sulaiman and Abdullah (2017); and Wattanachaiyingcharoen et al. (2011); Wattanachaiyingcharoen et al. (2016); Wijekoon et al. (2012); Asri et al. (2020). Additionally, some studies combine visual counting and sweep net sampling, as shown in the study by Jaikla et al. (2020), and visual evaluation with aerial net sampling, as indicated in a study by Foo and Mahadimenakbar (2015). In addition, other methods were used in previous studies, such as visual counting (Prasertkul, 2018; Khoo et al., 2012; Faudzi et al., 2021) and aerial net (Sulaiman et al., 2017).

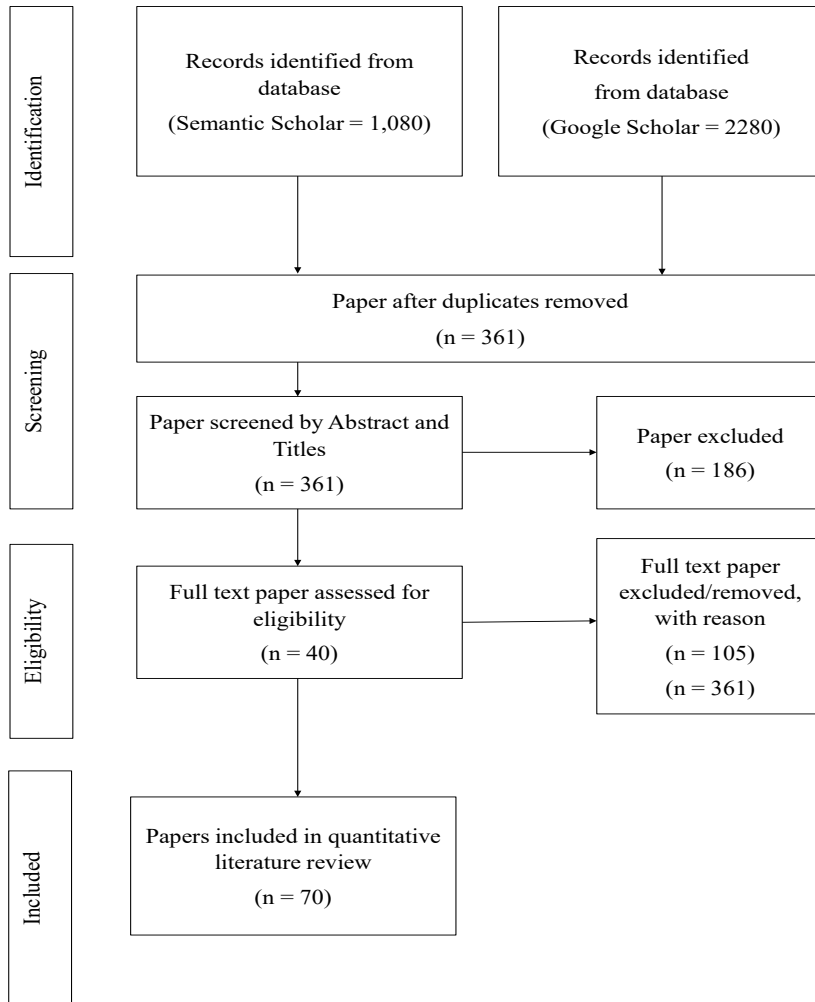


Figure 1. PRISMA methodology flowchart

Previous researchers preferred sweep nets because they are usually made of heavy material that can be dragged through dense vegetation without damage. This sweep net has the advantage of sweeping through vegetation to capture random insects that are not apparent, which is very useful when capturing adult fireflies at night. Meanwhile, aerial nets are rarely used, probably due to their durability; they are composed of several types of netting material and usually have a lightweight handle. Due to its lightweight feature and not being as thick as a sweep net, an aerial net is easily damaged if used in areas with dense vegetation.

DeWalt et al. (2015) suggested that sweep nets with a 38-cm net ring, 91-cm handle, and white muslin bag are highly suitable for sweeping insects out of riparian vegetation.

Sweep net sampling is excellent for determining species' existence and abundance in the field, but it does not provide a reliable estimate of larval density (Edde, 2022). In addition, the weakness in terms of methods applied by previous researchers was the relatively short study period. Ideally, a relatively long study period that may be more than six months to one year is very rational to do to be able to compare the population abundance of fireflies in each different year. So, the researcher will get complete data for one year and cover for each season within that year.

Not many past studies have used the Geographic Information Systems (GIS) and Spatial Analysis approach. Most only used the Global Positioning System (GPS) to mark a congregating station/vegetation of fireflies. Some previous studies use very simple mapping techniques, such as Wijekoon et al. (2012); Wattanachaiyingcharoen et al. (2011); Sartsanga et al. (2015); Jusoh et al. (2010b); Jusoh et al. (2011); Asri et al. (2020); Prasertkul (2018); and Shahara et al. (2017). All the mapping shows the sampling area and the species found there. A study can be said to be more advanced in the mapping technique compared to other previous studies by Jusoh et al. (2012). In the study, they used the land-use spatial analysis of satellite images to investigate the changes taking place to the mangroves on which the fireflies depend. The study conducted by Abdullah et al. (2020) should apply the inverse distance weighting (IDW) technique to obtain a more precise and more exciting data presentation on the relationship between water quality parameters and firefly population.

Several GIS techniques can be used to show the population density of fireflies. First, the hotspot technique shows which area (display tree, sampling point) is the hotspot area (focus) of fireflies, as well as which vegetation species is the primary choice of fireflies to be selected as a display tree. Second, buffering analysis. Buffering can be used to determine the area covered by fireflies in a particular location by indicating at what distance can affect the population distribution of fireflies. As for water quality, among the GIS techniques used is inverse distance weighting (IDW). This technique has been used to delineate groundwater pollutants' area distribution and obtain the spatial dissemination of water quality parameters of the river near the firefly habitat. Finally, data visualization in mapping is easy to comprehend and interpret. Thus, it is suggested that more techniques than GIS applications be used in studies related to the population abundance of fireflies.

Furthermore, the data analysis techniques used in the study of Shahara et al. (2017), i.e., Percentage Cover Estimation (PCE), provide an abundance index (Jusoh et al., 2010b; Nada et al., 2012; Shahara et al., 2017), but it does not indicate how many males are present in each congregation. Digital night photography-image analysis (Khoo et al., 2012) and photo visual analysis using a high-resolution camera (720 pixels HD) (Faudzi et al., 2021) may provide a more reliable estimate. However, it requires meticulous setups on a well-positioned platform that may not be available for every congregation. Another disadvantage of using this technique (Prasertkul, 2018) is that long-exposure photography is sensitive

to movement. So, it will be hard to get a clear picture when the fireflies are moving, or the trees sways. Therefore, manual flash counting was still ideal for studies involving fireflies.

Biotic Factors

Several biotic factors can influence the abundance of fireflies. Human activities or natural calamities, for example, might endanger the snail the firefly larvae feed on (Foo & Mahadimenakbar, 2015). These are because certain riparian vegetation species, such as *Sonneratia caseolaris*, *Hibiscus tiliaceus*, *Nypa fruticans*, *Acrostichum aureum*, *Areca cathechu*, *Oncosperma tigillarum*, and *Ficus* sp., are frequently found in riparian habitats and are associated with fireflies in Peninsular Malaysia and Thailand (Khoo et al., 2012; Prasertkul, 2018; Juliana et al., 2012). The larvae of fireflies are predators of the tiny snails *Cyclotropis carinata* that inhabit the riverbanks (Nada & Kirton, 2004). Their larvae can be found in mangroves and mangrove fringes where *Acrostichum aureum*, *Acanthus ebracteatus*, and *ilicifolius* are present. *Colophotia praeusta*, on the other hand, is a scrubland species. Their adults are found in damp places with few trees and dense grass, among grasses and weeds. Meanwhile, *Pyrocoelia* sp., *Stenocladus* sp., and *Diplocladon* sp. were discovered in secondary forests in Singapore. Adult *Pyrocoelia* sp. likes to visit forest edges in open and closed areas (Chan, 2012). However, in northern Thailand, one species of firefly, *Asymmetricata circumdata* (Motsch.), can be found in disturbed regions such as urban and cultivated areas, but the population is still limited in comparison to natural environments (mixed deciduous forests) (Wattanachaiyingcharoen et al., 2011).

Most *Pteroptyx* spp. have a riparian environment supporting mangroves but not necessarily a mandatory association with mangroves or any particular species. For example, *Pteroptyx galbina* was found up to 30 km from the sea, whereas *P. bearni* Olivier is found in mangroves and other riverside flowering plants (Jusoh et al., 2018). It has been found that most species of firefly prefer to display trees along riverbanks in mangrove zones (Jusoh et al., 2011). Nevertheless, these species' selection of display trees is not necessarily from the same species (Chey, 2004; Ohba & Wong, 2004) since firefly species were discovered to appear in other vegetations species in Sabah's riparian area, including *Rhizophora apiculata*, *Clerodendrum inerme*, *Glochidion littorale*, *Bruguiera parviflora*, and *Excoecaria indica* (Chey, 2004; Mahadimenakbar & Fiffy Hanisdah, 2016). It was demonstrated in a study by Li et al. (2013), who discovered significant differences in the richness and abundance of ground-dwelling arthropods beneath various shrub species. The general impression was that *Sonneratia caseolaris* (L.) Engl. was the mangrove tree. (Sonneratiaceae) was much preferred as a display tree, but it depends on the health condition of this vegetation (Shahara et al., 2017).

While according to Chey (2004), *P. tener* is not specific to which tree it roosts; rather than specificity, its preference is determined by tree suitability. Additionally, Ohba and

Wong (2004) stated that *Pteroptyx* congregations do not require a specific plant species because leaf size, density, and arrangement of leaves, as well as tree location, are potential considerations in display tree selection. In the investigation that has been done on the foliage of the firefly trees, scars, lesions, and tunnels were visible on several leaves, which could have been made during adult firefly feeding (Othman et al., 2018). Klias River (Malaysia Borneo, Sabah) has some trees covered in sparkling fireflies. The trees include the Dungun tree, the mangrove tree Bangkita, and the *Rhizophora apiculata* Bl. (Rhizophoraceae), and the *Excoecaria indica* (Willd.) Muell. Arg. (Euphorbiaceae) tree, also known as the Ligura (Chey, 2004). Chey (2004) also noted the presence of nipa and sago trees near the Klias River, ideal habitats for firefly larvae. The higher firefly larval density in Sago palm groves than in oil palm plantations has been attributed to several factors: 1) The sago patch was cooler, more humid, and shaded; 2) The orchard and oil palm plantation had higher mean air temperatures and lowered mean relative humidity than the sago patch; 3) The orchard had significantly higher soil temperature at a depth of 5 cm than the oil palm plantation and sago patch; and 4) The orchard had the highest photon flux density and the sago patch had the lowest (Kirton et al., 2006). It shows the interconnectedness between the firefly and the river ecosystem. Other possible explanations include the likelihood that the Chukai River in Terengganu, Malaysia, has a low insect population due to the vegetation, *B. racemosa*, that dominates the Chukai River's banks. This plant species is known to contain insecticides (Saponins) capable of repelling insects' presence (Osman et al., 2017).

Most fireflies have been found in *Sonneratia caseolaris* (L.) Engl., (Jusoh et al., 2011), but this species was also found on other display tree species, including *Gluta velutina* Blume, *Hibiscus tiliaceus* L., *Xylocarpus granatum* J. König, *Avicennia alba* Blume, *Rhizophora apiculata* Blume, *Excoecaria agallocha* L., *Barringtonia racemosa* (L.) Spreng., *Bruguiera gymnorhiza* (L.) Lam. and *Nypa fruticans* Wurmb. However, in Peninsular Malaysia, oil palm plantations are encroaching on riverbanks, posing a threat to firefly habitat (Jusoh & Hashim, 2012). Because biotic factors such as mangrove assemblages have a close relationship with firefly abundance, it is critical to protect mangrove swamp ecosystems to maintain their ecosystem functions (Jusoh et al., 2010a). In Thailand, habitat fragmentation is assumed to be responsible for the decline in the population size or local extinction of *Luciola aquatilis* Thancharoen fireflies, as it restricts the firefly dispersal range (Thancharoen, 2007). In addition, several studies conducted in Sabah, Malaysia, such as those conducted on Sakar Island off the coast of Lahad Datu Sabah, found that two firefly species, *Pteroptyx bearni* and *Pteroptyx gelasina*, selected *Scyphiphora hydrophyllacea*, *Rhizophora apiculata*, *Rhizophora mucronata*, and *Rhizophora stylosa* as their display trees (Chey, 2011). In the Garama River, Beaufort fireflies *Pteroptyx bearni*, *Pteroptyx malaccae*, and *Pteroptyx tener* prefer *Rhizophora apiculata*, *Ficus microcarpa*, and *Clerodendrum inerme*, respectively (Chey, 2010); however, in the Klias River, Beaufort, these three

species of fireflies are only found in two types of vegetation, namely *Rhizophora apiculata* and *Glochidion littorale* (Chey, 2010). *P. gelasina* and *P. bearni* in Trayong, Tuaran, chose to be in *Scyphiphora hydrophyllacea* and *Lumnitzera littorea* vegetation (Chey, 2009). Finally, *P. gelasina* and *P. bearni* species discovered in the Sepilok Forest Reserve, Sandakan, chose *Lumnitzera littorea*, *Rhizophora apiculata*, *Scyphiphora hydrophyllacea*, and *Rhizophora mucronata* vegetation as their habitat (Chey, 2008).

Meanwhile, because mangroves provide an essential ecosystem for larvae that feed on snails in the intertidal zone, fireflies and mangroves are closely associated (Nagelkerken et al., 2008). *Pteroptyx* species are classified as semi-aquatic fireflies since they spend their larval stage on muddy riverbanks and may survive for a short period underwater (Thancharoen, 2007). For instance, the snail *Cyclotropis carinata* (Assimineidae) is the primary prey for the firefly larvae, which can be found in tidally inundated areas of riverbanks. Besides entering the shells of the snails and injecting a paralyzing toxin and an enzyme into their soft body tissues to aid in feeding, these larvae are also capable of entering their prey shells (Nagelkerken et al., 2008). It is proven that the prey of snails inhabiting damp areas in mangrove swamps is crucial for the survival of fireflies in the larval stage. This larval stage is the most vital and essential stage for fireflies because they spend a significant amount of time in this stage, which is 97.83 days, dependent on the river water (Loomboot et al., 2007). Near Nipah and Sago palm trees, the larvae, which eat river snails, are often found 5 to 30 meters away from the display trees (Loomboot et al., 2007). Firefly larval density was more significant in Sago palm groves than in oil palm stands, owing to the supply of food (*Cyclotropis carinata* snails) in the patches of sago, compared to few or no snails in oil palm plantations (Kirton et al., 2006). According to Cheng et al. (2017), the adult firefly will also travel further inland, searching for food sources (*Heritiera littoralis*). Overall, the life cycle of *Pteroptyx malacca* Gorham species lasted about 12.15 days during eggs, larvae (97.83 days), pupae (9.83 days), and adults (12.33 days) (Loomboot et al., 2007). *Pteroptyx* larvae feed on mangrove snails, and after they fully develop, the larvae will construct a tiny cell in the mud for pupation (Loomboot, 2007; Loomboot, 2008). *S. caseolaris*, which can be found in the riparian area, has unique and different structural architecture; its complex structure and larger-sized vegetation can provide more resources in the form of leaves and litter for insects to thrive on, particularly food sources (Abdullah et al., 2019).

As for the *Pteroptyx valida*, their life span ranges from 107–228 days, with lasted about 16–25 days during eggs, larvae (76–168 days), pupae (5–13 days), and adults (6–15 days) (Jaikla et al., 2020). Their larvae and some snails that they feed on brackish water are favored in the intertidal zone (Chan, 2012) (Figure 2). The preference for *S. caseolaris* could be explained by the nectaries found on young *S. caseolaris* trees, which supply nutrition for adult fireflies (Juliana et al., 2012; Nallakumar, 2003) and catalyze a series

of chemical reactions within the firefly's body, resulting in photon flashes (synchronous flashing) (Nallakumar, 2003). Adult fireflies, for example, use the *S. caseolaris* trees that line the Selangor River's riverbanks as mating places and food sources due to the presence of sugar in the sap of these trees (Nada et al., 2009). Othman et al. (2018) discovered a unique food canal running from the tip to the end of *P. tener*'s mandible, which confirms it. The mandible tip may be used as piercing equipment by *P. tener* to suck plant sap for food. Additionally, evidence from this species' digestive tract revealed that these species have a tiny crop, a large ventriculus, and a long intestinal tract, all suited for a liquid feeder insect. To sum up, *S. caseolaris* (Berembang) was the most preferred display tree in Peninsular Malaysia by the *Pteroptyx tener* (Jusoh et al., 2010a; Jusoh et al., 2010b).

At Mae Wong National Park and in the evergreen forests of Thailand, *Asymmetricata circumdata* have been found, which are favorite places to find land snails, earthworms, and soft-bodied insects that could be a helpful food supply for firefly larvae (Wattanachaiyingcharoen et al., 2011). In Singapore, mangroves are home to the *Pteroptyx valida*. Adults of this species prefer *Avicennia alba* mangroves, but they can also be found in *Rhizophora apiculata* and *Sonneratia alba* mangroves. In the mangrove area of Nakhon Sri Thammarat, Thailand, which is closer to Malaysia and linked to Surat Thani, no *Pteroptyx tener* was found. It is probably due to the lack of ecological linkages in coastal habitats suitable for fireflies, owing to the fragmentation of mangrove areas in this country, which has influenced the occurrence trend of *P. tener* (Sriboonlert et al., 2015). The study by Jaikla et al. (2020) shows that display trees with open canopies located at river bends are prominent features for fireflies.

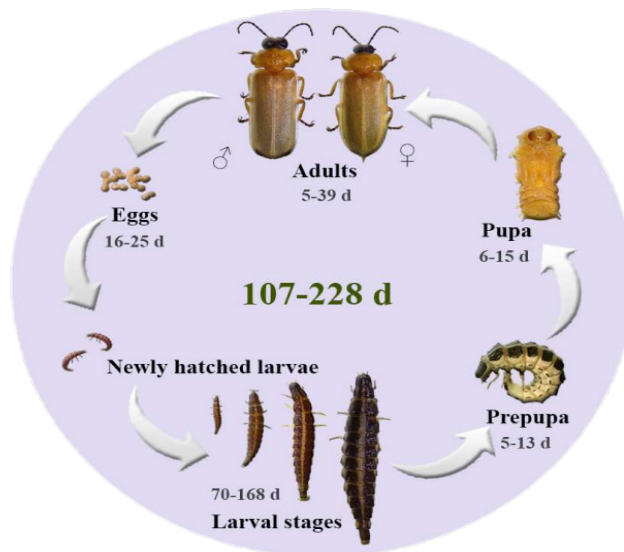


Figure 2. Life cycle of *Pteroptyx valida* in Thailand (Jaikla et al., 2020)

Abiotic Factors

Wind speed is one of the abiotic factors that influence the firefly population. According to a study by Asri et al. (2021), wind speed significantly impacted the temporal variation of fireflies. They also discovered that the population size of fireflies in Sungai Rembau in Negeri Sembilan, Malaysia, decreased from January to April 2018 and varied due to wind speed changes. Their findings are similar to those of Abdullah et al. (2019), who reported that wind speed had influenced the population size of fireflies at the same study area (i.e., Rembau River). Conversely, in the same study, Abdullah et al. (2019) also discovered that wind speed had a significant negative association with insect abundance and diversity in the Sepetang River and Chukai River. The difference may be due to geographical factors of the study area where Sungai Rembau Negeri Sembilan was exposed to Southwest monsoon types with a wind speed of 15 knots stronger than the wind in the Sepetang River and Chukai River (Asri et al., 2021). The study by Jaikla et al. (2020) on the influence of wind direction and speed on the horizontal distribution of *Pteroptyx* spp. in Thailand.

Bang Bai Mai, Surat Thani; Phetchaburi River, Phetchaburi; Khae, Khlong Thom, Krabi; and Pak Phanang, Bang Kong Khong, Nakhon Si Thammarat) revealed that firefly species preferred to perch on tree areas facing away from the current wind direction (Figure 3). 85% of this firefly species sat more than 45° to either side of the wind direction. 13.1% of the fireflies perched closer to the current wind direction (within 45° on both sides), and 1.9% of the fireflies perched directly facing the wind.

Next, in terms of the soil condition, female fireflies usually fly to the muddy cliffs behind the vegetation after mating and laying their eggs in damp soil (Nada et al., 2008). Therefore, it is suggested that to lay eggs, female fireflies require damp soil. According to Ohba and Sim (1994), excessive water is beneficial to the larvae of the *Pteroptyx Valida* and encourages the population to increase. In addition, firefly eggs require moist soil and shaded areas, such as those provided by *Rhizophora* sp., to ensure that the eggs will not become damaged when exposed to high temperatures and dry conditions (Jusoh et al., 2010a). *Pteroptyx valida* larvae were found in the mangrove area of Singapore, where they preferred moist, wet soil and damp leaf litter composed primarily of *Hibiscus tiliaceus* leaves. *Pyrocoelia* sp., *Stenocladus* sp., and *Diplocladon* sp. larvae preferred moist, wet soil and leaf litter on forest fringes (Chan, 2012). The *P. tener* Thailand was only spotted in a brackish river along the Tapi River in Phunpin district, Surat Thani. *Pteroptyx* fireflies in this area were present throughout the year, with the most significant proportion of adult fireflies seen in October and December (Sriboonlert et al., 2015).

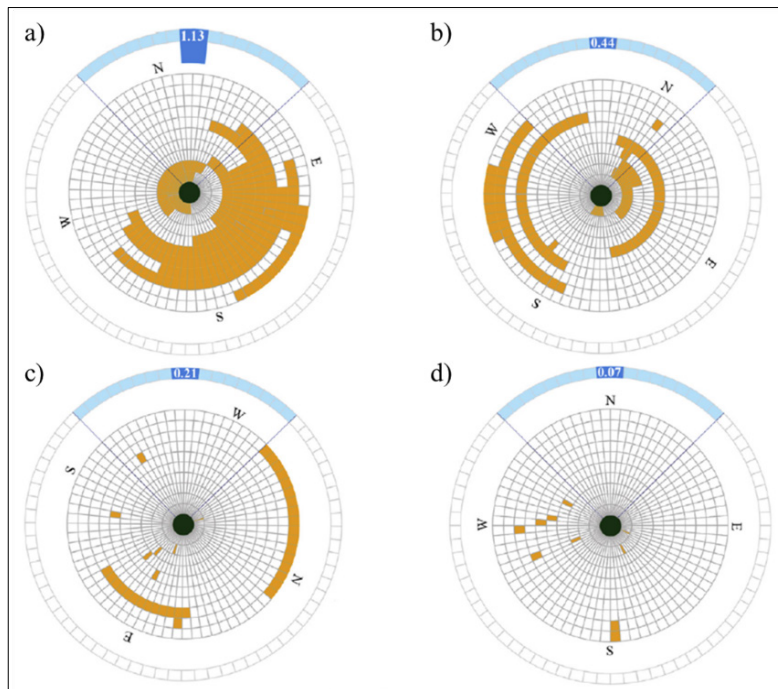


Figure 3. The effect of wind direction on the perching position of *Pteroptyx* spp. in Thailand: a) Bang Bai Mai, Surat Thani; b) Phetchaburi River, Phetchaburi; c) Khae, Khlong Thom, Krabi; and d) Pak Phanang, Bang Kong Khong, Nakhon Si Thammarat (Jaikla et al., 2020)

Notes: Concentric Circles - Display Trees; Orange Bands - *Pteroptyx* Spp. Perching Positions; Dark Blue Bands (In the Outermost Circle) - Wind Direction and Wind Speed; Taller Blue Bands Indicate Stronger Wind Speed

Air temperature has also been proven to have a spatial impact on firefly populations. The size of the firefly population has been reported to have decreased and varied as a result of temperature changes (Asri et al., 2021). The flash interval of fireflies is greatly influenced by air temperature; the flash interval increases when the air temperature falls. Furthermore, the regressions of flash interval on air temperature changed considerably between locations but not between years (Iguchi, 2002). According to Abdullah et al. (2020), ambient air temperature negatively correlates with firefly abundance in Sungai Niah and Sungai Sibuti, Miri, Sarawak, Malaysia, indicating that the firefly is susceptible to higher temperatures. The ambient air temperature in these areas ranged from (24.0°C to 27.9°C). About 2000 fireflies from the beetle order Coleoptera and Lampyridae families are consistently found in varied temperate and tropical climates worldwide (Wang et al., 2007). Hermann et al. (2016) found a trend in firefly activity, indicating that temperature accumulation is indeed a driver of firefly activity. The temperature accumulation of roughly 800 degrees (base 10°C) is where activity peaks. The model also reveals that precipitation

extremes delay thermally moderated firefly activity. As for the firefly larvae, the optimal temperature for larval activity is 18-30°C (Wang et al., 2007). Air temperature ($27.6 \pm 0.7^\circ\text{C}$) and relative humidity ($82.7 \pm 3.2\%$) were found to be important in determining the abundance of the firefly population along the Sungai Sepetang riverbanks in Kampung Dew, Perak, Malaysia, particularly at night (Sulaiman et al., 2017). Although most fireflies are found in areas with high humidity, one species is known to live in the desert, namely the (Lampyridae: *Microphotus Octarthrus* Fall) which can be found in pinyon-juniper and juniper-oak ecosystems between 500 and 2,000 meters in Arizona, New Mexico, West Texas, and Utah (Usener & Cognato, 2005).

Conversely, the low temperature resulted in a large distribution of fireflies. It was attributed to the most significant number of fireflies collected at the sampling station at 27.3°C and 28.8°C compared to the sampling station with the highest mean temperature value of $29.95 \pm 0.65^\circ\text{C}$ (Faudzi et al., 2021). Firefly Percentage Cover Estimation (PCE) of both the right and left riverbanks in Bernam River, Selangor, Malaysia, was shown to have weak and insignificant associations with the abiotic parameters (temperature, relative humidity, wind speed, water salinity, total dissolved solids, conductivity) (Shahara et al., 2017).

Firefly larvae are discovered hiding in cracks or under emarcid leaves, with the head retracted inside the pronotum and using the caudal grasping organ to cling to the substrate or plants during the day- an indication that they prefer low temperatures and high humidity. Then, the larvae began to crawl slowly after sunset (7 p.m. to 8 p.m.) (Wang et al., 2007). On the other hand, adults hide in tiny holes on the ground or perch at the bottom of leaves to escape sunlight throughout the day. Adults began to glow at sunset when the ambient light intensity was reduced. Glowing activity peaked around 1 hour later, when ambient light intensity was about 0 Lux, and generally ceased at 5:00 a.m. the next day. A study conducted in mainland China in 2003-2005 by Wang et al. (2007) showed that the glowing activity of fireflies decreased when there was bright moonlight and intense artificial light or windy, rainy, or cooler.

Meanwhile, it was in contrast to the findings of Foo and Mahadimenakbar (2015). They found that moonlight intensity does not influence on firefly abundance in Teratak River, Sabah, Malaysia, during the full moon and the night of the new moon. Similar to Shahara et al. (2017) findings, there are no statistically significant differences in firefly abundance between the full moon and new moon phases in Bernam River, Selangor, Malaysia. The differences in the study's findings may be because the study period used by Foo and Mahadimenakbar (2015), which was March to April 2014 (two months), and Shahara et al. (2017), which was February to April 2015 (three months), is comparatively short and insufficient to comprehend and make comparisons firefly abundance during the full moon and new moon nights. In opposition to Wang et al. (2007), field observations were made

over a more extended period, from 2003 to 2005, including daily visits during the summer and autumn. The difference may also be influenced by ambient light intensity since even when the full moon occurs, the light intensity may be obscured by thick and dark clouds and haze and smoke in the atmosphere.

The rainy season is ideal for firefly larvae and snails to grow and develop. This condition would increase the population of these species in the months following the rainy season (Nada et al., 2012). In northern Thailand, firefly diversity was influenced by seasonal variation. Some of them appeared during the winter when the temperature was lower at high altitudes (*Luciola* sp.3). It implied that fireflies could survive at high altitudes (Wattanachaiyingcharoen et al., 2016). *Luciola nicollieri* in colder, wetter regions of Uva, Sabaragamuwa, and the North-Western Province of Sri Lanka are evidence that firefly species favor cold climates with high rainfall distribution. Rainfall in Sri Lanka may significantly impact the diversity and abundance of firefly species (Wijekoon et al., 2012). *Luciola chinensis* (under the *Luciola praeusta* complex) was also found in the Southern, Uva, and Sabaragamuwa Provinces, which favored wet climates. However, *L. chinensis* was rarely reported in heavily urbanized areas (Western and Central regions), despite the area being likewise wet (Wijekoon et al., 2012). Meanwhile, *Pteroptyx asymmetria* is restricted on both coasts of southern Thailand, which shares a similar climate with Malaysia (Jaikla et al., 2020) with this species has been documented only in western Peninsular Malaysia (Jusoh et al., 2018).

Wattanachaiyingcharoen et al. (2016) stated that Northern Thailand's highlands were home to numerous fireflies. The seasonal appearance of these firefly species from the Subfamily Lampyrinae and Subfamily Luciolinae can be seen in Table 2. According to the evidence collected by Wattanachaiyingcharoen et al. (2016) in their study (Table 2), some fireflies had seasonal specificity. For instance, the *Diaphanes* sp. 3 and *Luciola* sp. 3 species only appeared in winter. *Pyrocoelia* sp. 2 and *Luciola trilucida*, on the other hand, appeared only during the wet (rainy) seasons. In addition, some firefly species in Northern Thailand, such as *Pyrocoelia analis* and *Luciola indica*, have a broader adult seasonal appearance, appearing from summer to rainy seasons. This record demonstrates a species preponderance in ambient environments, particularly *Pyrocoelia* sp. 2 and *L. trilucida*, that tend to appear in wet conditions. Another study found similar results, showing that *Asymmetricata circumdata* fireflies were found in various habitats in the north of Thailand between the end of April and the beginning of August. However, from the end of April to mid-May, when the weather was most likely to be rainy, the most significant number of fireflies were spotted (Wattanachaiyingcharoen et al., 2011).

Table 2

The seasonal appearance of firefly species was found in 83 study sites in the highland areas of Northern Thailand (Wattanachaiyingcharoen et al., 2016)

Species	Seasonal Appearance
Subfamily Lampyrinae	
<i>Diaphanes</i> sp.2	Early Rainy (Late May)
<i>Diaphanes</i> sp.3	Winter (December–February)
<i>Diaphanes</i> sp.4	Mid-winter (January)
<i>Lamprigera yunnana</i>	Late Rainy—Winter (October–January)
<i>Pyrocoelia analis</i>	Late Summer—Rainy (Early May–September)
<i>Pyrocoelia</i> sp.1	Winter (December–February)
<i>Pyrocoelia</i> sp.2	Rainy (June–September)
Subfamily Luciolinae	
<i>Abscondita anceyi</i>	Summer—Early Rainy (March–May)
<i>Abscondita chinensis</i>	Rainy—Winter (June–December)
<i>Asymmetricata circumdata</i>	Summer—Rainy (March–September)
<i>Asymmetricata ovalis</i>	Rainy (June–September)
<i>Curtos cerea</i>	Rainy (June–September)
<i>Luciola curtithorax</i>	Rainy (June–September)
<i>Luciola indica</i>	Late Summer—Rainy (Early May–September)
<i>Luciola triluclida</i>	Rainy (June–September)
<i>Luciola</i> sp.3	Winter (December–February)
<i>Pygoluciola</i> sp.1	Early Rainy (Late May)
<i>Trisinuata</i> sp.2	Late Summer—Rainy (Early May–September)
Unknown genus and species	Late Winter (January–February)

Temperature and humidity did not demonstrate a significant association with insect communities, according to a study by Abdullah et al. (2019); however, warmer and less humid environments can contribute to insect mortality. Over three years, from January 2006 to April 2008, the relatively consistent and slightly varying average monthly temperature and relative humidity did not appear to alter the increasing trend of the adult firefly population. During that period, the temperature ranged between 26.4–28.4°C, while the relative humidity was between 78.3–85.7% (Khoo et al., 2012). Meanwhile, Nada et al. (2012) discovered a remarkably steady average monthly temperature (26.4–28.4°C), relative humidity (78.6–84.9 %), and water quality [68 (slightly polluted) - 86 (clean)] with little variability from January 2006 to April 2007, seemingly scarcely affecting any trend in the adult firefly population. It was also discovered that air humidity geographically

affected the firefly population. Temperature variations have been seen to cause a reduction and fluctuation in the population size of fireflies (Asri et al., 2021). For firefly larvae, 90% or higher relative humidity is ideal for larval activity (Wang et al., 2007). It is also supported by Nada and Kirton (2004), who argued that humid environments might benefit larval growth and the host snail population. It is because the life cycle of *Pteroptyx tener* is expected to take around three months to complete.

Table 3

Specimens of Pteroptyx species collected in Thailand during the period 2012 to 2015 (Sartsanga et al., 2018)

Region	Number of specimens			
	<i>Pteroptyx asymmetria</i>	<i>Pteroptyx malaccaae</i>	<i>Pteroptyx valida</i>	<i>Pteroptyx tener</i>
East (Thai Gulf)	0	118	72	0
Central (Thai Gulf)	0	51	30	0
South (Thai Gulf)	22	128	43	30
South (Andaman)	65	2	5	0

Sartsanga et al. (2018) reported that only *P. malaccaae* and *P. valida* were present in East and Central Thailand, and no *P. asymmetria* was identified in those regions (Table 3). In contrast to the firefly species found in the South, *P. asymmetria* was the only species. The capability of *P. malaccaae* and *P. valida* to tolerate lower humidity and more fluctuating temperature conditions in the eastern and central areas (winter, hot, and rain) than in the south (rain and heat) may explain their prevalence in the East and Central areas. The most abundant *Asymmetricata circumdata* species in Thailand was found in the mixed deciduous forest of Mae Wong National Park at an altitude of 289 MSL (Mean Sea Level), with a population of more than 1,000 individuals per site. The evergreen forests in the country with an altitude of 950 MSL had an average firefly population of 100 individuals per site. This firefly species have also been found in evergreen forests throughout the year. It could be because the temperature is favorable throughout the year. As a result, food sources are available for the larvae of this species of fireflies, particularly in forest areas with less pesticide accumulation and less electric light. These are the factors that contribute to the natural reproduction of this firefly species. Compared to lowland and disturbed habitats, such as urban and agricultural areas, fewer individual species are reported (Wattanachaiyingcharoen et al., 2011). Furthermore, electric lights in metropolitan areas can disrupt firefly sexual communication (Thancharoen, 2007). It is supported by Thancharoen (2001), who found *A. circumdata* in the tropical rain forest of Pha Kluai Mai Waterfall, Khao Yai National Park, Thailand, at approximately 680 meters MSL.

In addition, water salinity (NaCl) can alter the soil where fireflies lay eggs and hatch as larvae (Abdullah et al., 2019). In Sungai Rembau, Malaysia, the water salinity indicated only a marginally negative association with firefly abundance spatially and temporally. The firefly population in this area had an optimal level of water salinity, which peaked in January 2018 to March 2018 and June 2018 to August 2018. In line with this event, the population of fireflies likewise peaked in the downstream area of the river (Asri et al., 2021). The salinity of the water is significant for the growth of aquatic and semi-aquatic insects, including the population of fireflies. A relative trend of rising insect abundance with decreasing salinity value has been seen in Malaysia's Sungai Sepetang, Sungai Rembau, and Sungai Chukai. As most larval growth occurs in the water, the river's salinity must be maintained within a tolerable limit (Abdullah et al., 2019). By contrast, Khoo et al. (2012) found that a significant rise in salinity in Selangor River, Malaysia, did not affect the population of fireflies residing in *Sonneratia caseolaris* along the riverbank. In addition, salinity may impact the soil where fireflies lay their eggs and hatch as larvae. However, the direct effect of salinity on the firefly has never been investigated before (Abdullah et al., 2019).

Faudzi et al. (2021) researched in March 2019 to investigate the association between seven water quality parameters and the abundance of firefly populations in the Cherating River, Pahang, Malaysia. According to the study's findings, two parameters, namely the potential of hydrogen (pH) and suspended solids (TSS), had no association with the firefly population. Aside from that, other parameters showed a correlated association between firefly abundance and water quality parameters. For example, there was a strong positive correlation between dissolved oxygen (DO) and the firefly population. Meanwhile, there was a strong negative correlation between the firefly population and water temperature, biochemical oxygen demand (BOD), chemical oxygen demand (COD), and ammonia nitrogen (NH₃-N). It implied that five water quality parameters, namely water temperature, DO, BOD, COD, and ammonia nitrogen, appeared to impact the firefly population abundance in the Cherating River. The study also found that the higher the temperature in a waterbody, the fewer fireflies in a particular region (Faudzi et al., 2021).

Meanwhile, the Sepetang River in Kampung Dew, Taiping, Perak contains a high concentration of heavy metals, which causes the river's water quality to deteriorate, which subsequently interrupts the life cycle of fireflies (Nada & Kirton 2004; Hazmi et al., 2017). Pollution and dam and embankment construction operations farther upstream, according to Nada and Kirton (2004), are among the causes of changes in the river water quality. These activities can eventually impair the survival of snails and riverbank plants near the firefly habitat. It suggests that water quality is one of the abiotic factors indirectly associated with firefly survival. The moderate decline in water quality in the Selangor River in December 2006 and December 2008 did not appear to affect the adult firefly population

in the following months (Khoo et al., 2012). It suggests that a moderate decline in water quality may not affect the population of fireflies, but a significant decrease in water quality or contamination may cause a decrease in the population of fireflies. Leong et al. (2007) similarly addressed the effect of water quality on fireflies, emphasizing pesticide residues. Pesticide residues can also be toxic and have a detrimental impact on firefly larvae when they reside in intertidal zones on riverbanks flooded by river water during high tide. The levels of downstream pesticides in the Selangor River in 2002 and 2003 surpassed the US Environmental Protection Agency (EPA) guidelines for freshwater aquatic animals (Leong et al., 2007).

Figures 4 and 5 compare the monthly firefly abundance index at the Selangor River to the monthly maximum air pollution index (API) from May 2006 to April 2009. Figures 4 and 5 show that from 2006 to 2009, the month of October 2006 had the most petite firefly population sizes, disregarding the air quality levels. The high air pollution index (API) alone cannot explain this month's low population of fireflies. It may have influenced the population at its lowest in October 2006, when the API was unhealthy (Figure 5) (Khoo et al., 2012).

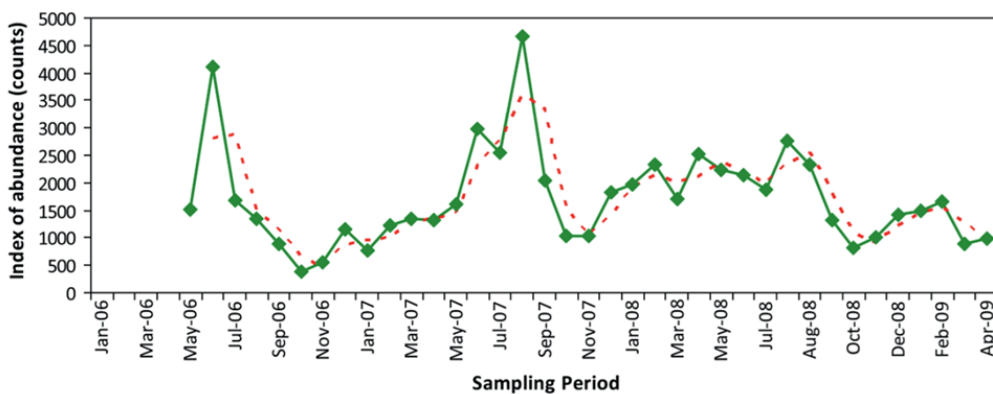


Figure 4. The overall monthly firefly population index for all locations from May 2006 to April 2009 (solid line) and a two-month interval moving average (dotted line) (Khoo et al., 2012)

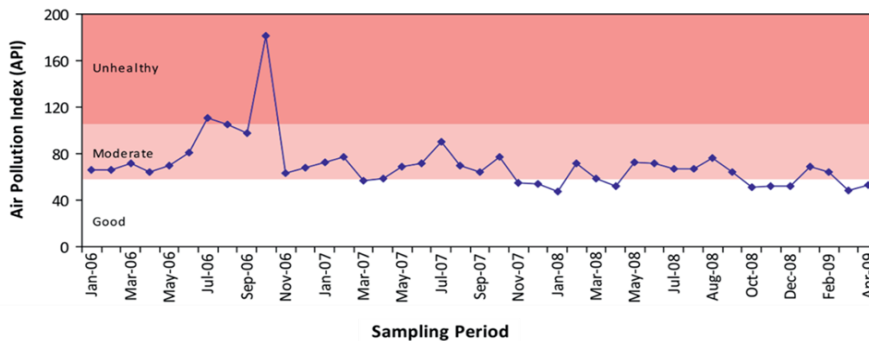


Figure 5. Monthly maximum air pollution index (API) in Selangor River (Khoo et al., 2012)

CONCLUSION

This study found that several abiotic factors are most likely to affect the population abundance of fireflies in Southeast Asia. Among them is water level in soil, air temperature, water humidity, rainy season, altitude, water salinity (NaCl), wind direction, wind speed, dissolved oxygen (DO), biochemical oxygen demand (BOD), chemical oxygen demand (COD), ammonia nitrogen (NH₃-N) and maximum air pollution index (API). However, few studies have focused on the specific parameters affecting this firefly species. Therefore, it is suggested that future studies focus more on how ecologically fireflies are affected as a result of environmental changes that affect abiotic in fireflies' habitat. This paper review also found that *Sonneratia caseolaris* (Berembang) remains the most preferred display tree because of many factors. Among them are 1) Display the tree's proximity to the water's edge; 2) appropriate arrangement of the leaf for mating purposes; 3) Presence of sap or nectar in the tree as a food source; 4) Display the tree's proximity to prey and food plants for larvae; and 5) Display tree's overall health (Jusoh et al., 2010b). Therefore, we suggest that more studies focus on the tree architecture of plant species in riparian zones or display trees.

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