The invasion of alien species *Miconia crenata* (Vahl) Michelang in disturbed/undisturbed lowland mixed dipterocarp and Kerangas forests in Sabah, Malaysia

Thian Yew LOKE[1,*], James A. MARGROVE[2], Berhaman AHMAD[1], Grace E. JIKIM[1], Alkinson C. ENDAWIE[1], Syahrir Mhd. HATTA[1], Anis P. ANDREW[1], Colin R. MAYCOCK[1]

*1. Faculty of Tropical Forestry, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia. 2. Department of Environmental Systems Science, ETH Zurich, Universitätstrasse 16, 8092 Zürich, Switzerland. *Corresponding author's email: lty.loke@gmail.com*

ABSTRACT: Understanding the factors that make a site susceptible to invasion is essential to mitigate the impacts of invasive alien plant species (IAPS) on biodiversity. *Miconia crenata* is one of the few IAPS that can colonize undisturbed tropical rainforests. In this study, we investigate the abundance of *Miconia crenata* in disturbed and undisturbed lowland mixed dipterocarp forest and Kerangas forests in Sabah, Malaysia. Three 400 m long transects were established within each of the four sites. The transects ran from the forest edge into the interior, and eight 25 m² plots were established at fixed distances along each transect. A further twenty 100 m² plots were established in each of the undisturbed sites of Kabili-Sepilok Forest Reserve. We found that the density of *Miconia crenata* was significantly lower along the transects in the Kerangas forest, compared to mixed dipterocarp forest. *Miconia crenata* densities were also significantly lower along transects in the undisturbed forest compared to the disturbed forest. Within the undisturbed sites, *Miconia crenata* was 13 times more abundant in the mixed dipterocarp forest compared to the Kerangas forest. This difference in *Miconia crenata* abundance between the two forest types is probably due to soil fertility, with fertile sites more susceptible to invasion by *Miconia crenata*.

KEY WORDS: Biodiversity loss, forest disturbance, invasive plant, Kabili-Sepilok Forest Reserve, Melastomataceae, tropical forest.

INTRODUCTION

Biodiversity loss is a major ongoing global crisis (Palombo, 2021). Next to habitat destruction, invasive species are one of the leading threats to biodiversity (Mollot *et al.*, 2017), although there is some debate on the impact of invasive plant species on biodiversity (Powell *et al.*, 2011). This is partly a result that the impacts of plant invasions vary among the different invaders, the different habitats and across different spatial and temporal scales (Powell *et al.*, 2011; Dai *et al.*, 2020). Understanding the factors that make an ecosystem susceptible to plant invasions is essential to mitigate the impacts on biodiversity, and a first step towards addressing Target 6 of the Post 2020 Global Biodiversity Framework (Essl *et al.*, 2020).

Anthropogenic disturbances are one factor that affects the likelihood of invasion (Fuentes-Lillo *et al.*, 2021). Previous studies have documented that disturbed sites have a higher susceptibility to invasion than undisturbed sites (Rejmánek *et al.*, 2013). While undisturbed lowland tropical rainforests are assumed to be resilient to invasion (Dawson *et al.*, 2015), Martin *et al.*, (2009) argue that this is largely a function of the longer turnover time of canopy trees. Furthermore, while forest invasions develop comparatively slowly under natural disturbance regimes, these are likely to increase due to other anthropogenic impacts on forest ecosystems (Turbelin and Catford, 2021).

The susceptibility of a site to invasion is also potentially influenced by soil fertility. Li and Norland (2001) suggested that in temperate forests, nutrient-rich soils area more susceptible to invasion than forest on nutrients poor soil. However, Davis *et al.* (2000) argued that susceptibility by invasive species is not entirely influenced by soil fertility but the availability of unused resources through the theory of resources fluctuations. These fluctuations rise in the availability of resources from increase disturbances, higher number of grazers, and the increase in nutrients. In this study, we determine the abundance of *Miconia crenata* (Vahl) Michelang (Melastomataceae) within disturbed and undisturbed lowland mixed dipterocarp and Kerangas forests in Sabah, Malaysia. These forest types represent two extremes of a soil fertility gradient (Sellan *et al.*, 2021). The aim of this study is to investigate whether forests on nutrient-rich are more susceptible to invasion by *Miconia crenata*. *Miconia crenata* is a highly invasive shrub and considered amongst the world's worst invasive alien species (Ibanez *et al.*, 2020). It is one of the few invasive species that can invade undisturbed continental tropical forests (Peters, 2001; Teo *et al.*, 2003). While there is debate on the impact of *Miconia crenata* on native species (Teo *et al.*, 2003; Peh, 2010), recent work suggests it has the potential to suppress regeneration of neighbouring plants (Döbert *et al.*, 2018; Wanigasinghe and Gunaratne, 2020), and may contribute to the long-term degradation of undisturbed lowland forests in Borneo (Waddell *et al.*, 2020a, b).
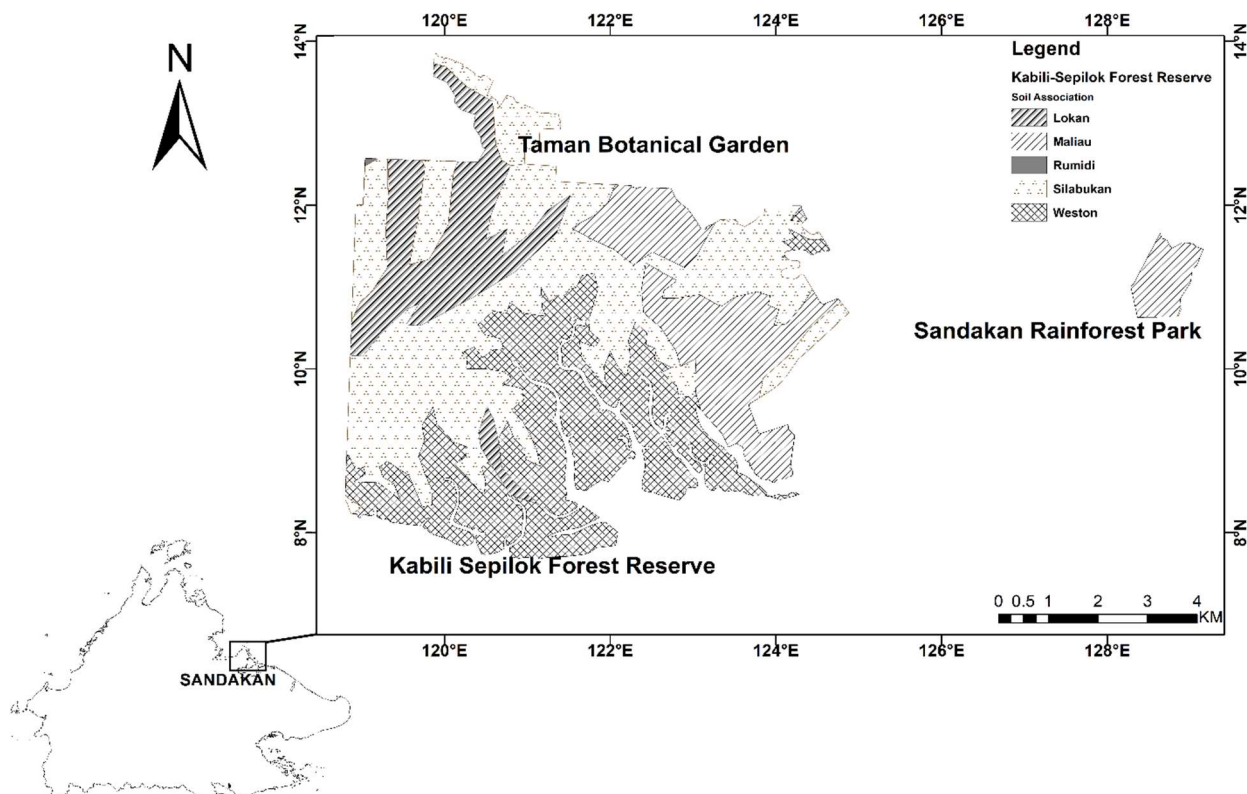
Fig. 1. Location of study sites and distribution of the different soil associations.

MATERALS AND METHODS

Study area

This study was conducted in disturbed and undisturbed lowland mixed dipterocarp and Kerangas (heath) forests of the Sandakan Peninsular within the northern part of Borneo Island, Sabah, Malaysia (Figure 1). The undisturbed sites were located within the Kabili-Sepilok Forest Reserve (5°51.25′N, 117°57.46′E), while the disturbed lowland mixed dipterocarp and disturbed Kerangas forest were in the Taman Botanical Sepilok (5°52.40′N, 117°56.51′E) and Sandakan Rainforest Park (5°51.02′N, 118°03.82′E), respectively. The Kabili Sepilok Forest Reserve is a 4475 ha Virgin Jungle Reserve surrounded by oil palm plantations and fruit orchards (Margrove *et al.,* 2015). The reserve is a mosaic of three distinct floristic associations lowland mixed dipterocarp forest on alluvium, hill dipterocarp forest and Kerangas forest. The distribution of these floristic associations is determined by the distribution of the soil association on which they occur. The three soil associations decline in overall fertility in the order Silabukan > Lokan > Maliau (Nilus *et al.,* 2011). For this study we focused on the lowland mixed dipterocarp forest using the soil association information on the Silabukan soil association (undisturbed nutrient-rich site), and Kerangas forests on the Maliau soil association (undisturbed nutrient-poor site). The Sandakan

Rainforest Park is an ~ 150-ha reserve, part of which has experienced anthropogenic disturbance. The soils are from the Maliau soil association. The forest is a disturbed Kerangas forest comprising a mixture of remnant Kerangas forest interspersed with areas dominated by *Acacia mangium* and other pyrophyllic plants (van de Ent *et al.,* 2021). Taman Botanical Sepilok is a logged-over lowland dipterocarp forest adjacent to the Kabili Sepilok Forest Reserve (Figure 1). The soils are from the Silabukan soil association, and the forest is a mosaic of secondary forests dominated by *Macaranga* spp. with remnant stands of dipterocarps. The climate of Sandakan Peninsular is aseasonal. The mean annual rainfall is 3136 ± 921 (SD) mm, with a mean annual temperature of 27.3 °C (Margrove *et al.,* 2015). There are no significant differences in rainfall totals between the two undisturbed sites (Mahali *et al.,* 2020).

Comparison of *Miconia crenata* abundance across a disturbance and soil fertility gradient

To investigate the relationship between soil fertility, forest disturbance and *Miconia crenata* abundance, we installed three 400 m transects within each forest type in November 2013 by 3 person-days per site. The transect ran from the forest edge into the interior, with a minimum of 250 m separating the transects. Along each transect eight 5 by 5 m² plots were established, the first plot was established at the forest edge and subsequent plots were

Table 1. Summary output of GLM with negative binomial distribution for the most parsimonious model with the lowest AICc.

Coefficient	Estimate coefficients	Standard error	z-value	*p*-value
Intercept	2.2582	0.0934	24.181	< 0.001
Distance	-0.0014	0.0006	-2.242	0.025
Forest Type(K)* Disturbance(U)	-1.2142	0.3419	3.551	< 0.001
Forest Type (K)* Distance	-0.0059	0.0011	-5.392	< 0.001
Disturbance(U)* Distance	-0.0598	0.0113	-5.281	< 0.001

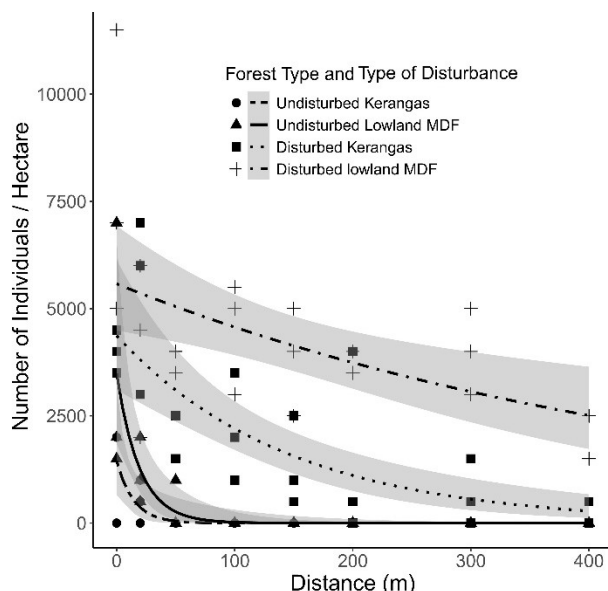(K) represents Kerangas forest, (U) represents undisturbed forest.

Fig. 2. *Miconia crenata* densities (individuals per hectare) within the disturbed and undisturbed lowland mixed dipterocarp and Kerangas forests. The points represent the number of individuals per hectare at different distances at each forest types and type of disturbances. The lines represent the predictions from the GLM with negative binomial distribution. The shaded areas represent the 95% confidence intervals for the prediction lines.

installed at distance of 20, 50, 100, 150, 200, 300 and 400 m from the forest edge. All *Miconia crenata* within the plots were counted.

Comparison of *Miconia* abundance within undisturbed mixed dipterocarp and Kerangas forests

The initial sampling showed that *Miconia crenata* abundance was low in the interior of the undisturbed forests, with preliminary analysis suggesting no detectable difference between the interior of the two undisturbed forest types. To account for this low abundance, we increased the sampling effort within this habitat and installed twenty 10×10 m² plots at randomly selected locations in September 2015 by 8 person-days within each forest type. Plots were separated by a minimum of 50 m and at least 100 m away from the forest edge. All *Miconia crenata* within the plots were counted.

Data analysis

Generalized linear models (GLMs) were used to investigate the relationship between forest type, disturbance, distance from forest edge and their interaction on *Miconia crenata* abundance. Forest type and forest disturbance were categorical data while distance was continuous. As the abundance data are counts, a generalized linear model (GLMs) with Poisson distribution was initially used. The GLM was fitted using the function "glm" in R version 4.0.2 (R Core Team, 2020). As this analysis indicates over-dispersion, a dispersion test was conducted using the function "dispersiontest" from the package AER version 1.2-9 (Kleiber and Zeileis, 2020). This showed a dispersion due to excessive zero counts in the dataset. To account for this, we fitted a negative binomial GLM. The negative binomial was fitted using the function "glm.nb" from the R package MASS version 7.3.51.6 (Ripley *et al.,* 2021). We used the function "glmulti" in the R package glmulti version 1.0.8 to select the most parsimonious model with the lowest corrected Akaike's information criterion for small sample size AICc (Calcagno and Mazancourt, 2010). Any model within two units ΔAICc of the lowest AICc were considered equivalent (Burnham and Anderson, 2002). For visualization, we present the model with the lowest AICc in Table 1, Figure 2.

The 10×10 m² plot data was analyzed using a similar approach, but with only one independent variable (forest type). The dispersion test showed a non-significant dispersion, so the GLM with Poisson distribution was considered the best fit model. We used the function "predict" to estimate the mean (± standard error) density of *Miconia* in each forest type (R Core Team, 2020).

RESULTS

Comparison of *Miconia crenata* abundance across a disturbance and soil fertility gradient

There was a significant difference in the abundance of *Miconia crenata* within the disturbed and undisturbed lowland mixed dipterocarp and Kerangas forests (z = -5.281, p < 0.001, Table 1). In the undisturbed forest, *Miconia crenata* was largely restricted to the forest edge and not recorded at distances greater than 50 m from the forest edge (Figure 2). In contrast, *Miconia crenata* was found throughout the transects in the disturbed forests, although the greatest densities were recorded at the forest edge (Figure 2). There was also a significant difference in *Miconia crenata* ability to penetrate the different forest types (z = -5.392, p < 0.001, Table 1). *Miconia crenata*

was found at higher densities at the forest edge towards the center of the forest in the lowland mixed dipterocarp forest compared to the Kerangas forest (Figure 2). There was also a significant interaction between forest type and disturbance (Table 1). Undisturbed Kerangas forest had lower *Miconia crenata* density.

Comparison of *Miconia crenata* abundance in undisturbed mixed Dipterocarp and Kerangas forests

With increased sampling effort in the undisturbed sites, we found a significant difference in *Miconia crenata* densities between the two forest types (Figure 3; z = -2.472, p = 0.013). *Miconia crenata* densities were 13-times greater in the undisturbed lowland mixed dipterocarp forest than the Kerangas forest. However, densities were low in both forest types, with an estimated 65.0 ± 18.0 and 5.0 ± 4.9 individuals per hectare in the undisturbed mixed dipterocarp and Kerangas forests, respectively. Few plots in either forest type contained *Miconia crenata*.
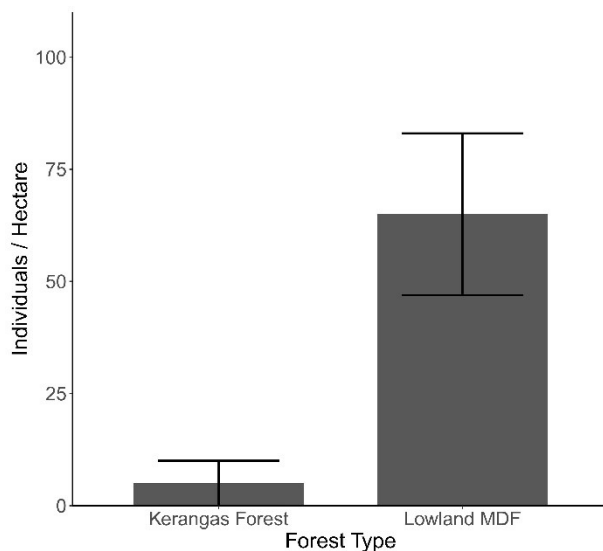

Fig. 3. *Miconia densities* within the undisturbed lowland mixed dipterocarp forest and Kerangas forest of the Kabili Sepilok Forest Reserve.

DISCUSSION

The abundance of an invasive plant species within an ecosystem is determined by the resource availability (light, water and soil fertility) of the site, the biotic resistance from resident vegetation, the species invasiveness and the propagule pressure (Zefferman *et al.,* 2015; Dyderski and Jagodziński, 2018). We found a significant difference in *Miconia crenata* densities between the two forest types (Figure 3), and greater penetration of *Miconia crenata* into the lowland mixed dipterocarp forest (Table 1, Figure 2). This is likely due to the differences in soil fertility between the sites, either

as a direct effect or via biotic interactions. Previous work has shown that the soils of the Kerangas forest are significantly less fertile than those of the mixed dipterocarp forest (Sellan *et al.,* 2021), with P and Fe probably limiting to plant growth (Sellan, 2019). For some invasive plant species, soil fertility is an important predictor of establishment (Huebner *et al.,* 2014). Soil fertility can affect the invasive species directly by reducing growth and survival on nutrient-poor sites or by reducing propagule pressure via reduced seed set (Lembrechts *et al.,* 2018). In the case of *Miconia crenata*, the differences in soil fertility between the sites could also affect its dispersal and establishment. The dispersal and establishment of *Miconia crenata* is mediated by wild pigs (Fujinuma and Harrison, 2012). Previous work has shown that pigs prefer richer habitats (Spitz and Janeau, 1995), and forage more extensively in wetter soils (Love *et al.,* 2017). As the Kerangas soils are less fertile, sandier, and potentially drier than the soils of the mixed dipterocarp forest (Sellan *et al.,* 2021), it is likely that foraging activities by pigs will be lower in these sites and this could impact *Miconia*'s ability to colonize these areas. Moreover, the theory of fluctuation of resources suggested that the disturbance by wild pigs can lead to resources availability that facilitate invasions (Davis *et al.*, 2000). While we selected sites that had similar annual rainfall total (Mahali *et al.,* 2020), differences in soil texture between the sites could affect water availability and the abundance of *Miconia crenata*. However, previous work has shown that *Miconia* has a broad climatic tolerance, is drought resistant, and grows in areas substantially drier than our sites (Rojas-Sandoval and Acevedo-Rodríguez, 2021). Similarly, differences in light availability between the two sites may contribute to the differences in *Miconia* abundance. Little information is available on light availability within these two forest types. However, the lower tree heights and structural complexity of the Kerangas forest suggests that it should have higher light levels than undisturbed mixed dipterocarp forest, making it more susceptible to invasion based on light alone (Le *et al.,* 2018).

The densities of *Miconia crenata* within the interior of the undisturbed forests of this study were more than order of magnitude lower than that report within the Pasoh Forest Reserve (Fujinuma and Harrison, 2012). While we found high densities of *Miconia crenata* at the forest edge (Figure 2), in contrast to the Pasoh studies we found little penetration of *Miconia crenata* into either of the undisturbed sites. Within the Pasoh Forest Reserve, wild pigs (*Sus scrofa*) are important for mediating the invasion of *Miconia hirta* into the undisturbed forest (Fujinuma and Harrison, 2012). In the case of our sites, the bearded pig (*Sus barbatus*) is the likely seed disperser (Waddell *et al.,* 2020a). Pig populations in the Kabili Sepilok Forest Reserve are likely to be lower than those of Pasoh due to hunting pressure by the surrounding

predominantly non-Muslim communities. While comparable data on pig densities within the two reserves is not available, other studies have shown that the encounter rates of *Sus barbatus* by camera traps are between 1.8 and 3.7 times lower within the Kabili Sepilok compared to other more isolated forest reserves in Sabah (Ross *et al.,* 2013).

Similar to past studies, we found higher densities of *Miconia crenata* at the forest edge and greater penetration of *Miconia crenata* into the disturbed sites (Table 1, Figure 2) (Waddell *et al.,* 2020b). This was particularly pronounced in the disturbed sites on fertile soils (Figure 2). Recent work suggests that edge effects are causing a decline in forest structure, up to ½ km from the forest edge, in the undisturbed lowland forests of Borneo (Qie *et al.,* 2017). This, coupled with degradation due to adverse climatic events and climate change (Margrove *et al.,* 2015; Turbelin and Catford, 2021), may make the undisturbed tropical forest of Borneo more susceptible to invasion by *Miconia* and other invasive species (Waddell *et al.,* 2020a, b). Monitoring invasive species in protected areas, conservation set asides and production forests is essential to gain an understanding of how they might impact the forest of Borneo and for devising strategies to minimize their impacts (Padmanaba and Corlett, 2014; Waddell *et al.,* 2020b). This work should be done as part of the national commitment to address Target 6 of the Post 2020 Global Biodiversity Framework (Erdelen, 2020; Xu *et al.,* 2021).

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