













Original Article

Leaf thickness and elevation explain naturalized alien species richness in a tropical mountain forest: A case study from Mount Gede-Pangrango National Park, Indonesia**Decky Indrawan JUNAEDI***  <https://orcid.org/0000-0001-5846-6135>;  e-mail: deqee82@gmail.com**Imawan Wahyu HIDAYAT**  <https://orcid.org/0000-0002-3619-1334>; e-mail: imawan.wahyu.hidayat@lipi.go.id**Muhammad EFENDI**  <https://orcid.org/0000-0002-9710-4775>; e-mail: muhammadefendi05@gmail.com**Zaenal MUTAQIEN**  <https://orcid.org/0000-0002-5132-5441>; e-mail: enal@musician.org**Musyarofah ZUHRI**  <https://orcid.org/0000-0002-2586-8872>; e-mail: ova_zuhri@yahoo.com**Taufikurrahman NASUTION**  <https://orcid.org/0000-0003-4467-5176>; e-mail: fiknas@yahoo.com**Fitri KURNIAWATI**  <https://orcid.org/0000-0002-2502-6229>; e-mail: upiet_v3@yahoo.com**Muhammad Imam SURYA**  <https://orcid.org/0000-0003-3900-7376>; e-mail: misuryao84@gmail.com**Lily ISMAINI**  <https://orcid.org/0000-0002-0853-183X>; e-mail: lily.ismaini@yahoo.com**Aisyah HANDAYANI**  <https://orcid.org/0000-0002-4101-2679>; e-mail: aisyahandayani88@gmail.com**Andes Hamuraby ROZAK**  <https://orcid.org/0000-0001-9641-5830>; e-mail: andes.hamuraby.rozak@lipi.go.id

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Abstract: Exotic plant invasion is one of the major causes of species extinction. In many contexts, mountainous forests are the last refuge for native species. There are several inventory studies conducted in mountainous and tropical forests in Indonesia. However, there are no studies yet on the factors that explain the abundance and richness of surveyed naturalized alien species. This study investigated whether the number of individuals and abundance-

weighted species richness (AWR) of naturalized alien plant species in the hiking-trail of Mount Gede-Pangrango National Park (MGPNP) forest area correlated with leaf traits (specific leaf area (SLA) and leaf thickness) and environmental factors (elevation, slope, and normalized difference vegetation index (NDVI)). We showed that leaf thickness and habitat elevation explained the AWR variations of naturalized alien species. We did not detect any important effect of leaf traits and environmental factors on the number of individuals per exotic species per plot. The influence of leaf thickness and habitat elevation indicates the important role of both biotic and abiotic factors on exotic species to develop a high species

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richness and become an invasive species in the tropical mountain forest ecosystem.

Keywords: Invasive species; Hiking trail; Cibodas Biosphere Reserve; Invasion ecology; SLA

1 Introduction

An invasive alien species (IAS) is defined as “alien species which becomes established in natural or semi-natural ecosystems or habitat, is an agent of change, and threatens native biological diversity” (IUCN 2000). IAS is one of the major threats to biodiversity loss (Gurevitch and Padilla 2004) and contribute to native ecosystem changes (Barney et al. 2013; Simberloff et al. 2013; Jeschke et al. 2014). Management of IAS is a global target in Convention on Biological Diversity (CBD) Aichi Biodiversity Target 9: “By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment” (Convention on Biological Diversity 2019). Therefore, invasive species surveillance, dispersal identification, containment, and eradication are crucial for biodiversity conservation and natural resources management in any ecosystem.

Plant invasion in tropical mountain forests contexts is one such concern. Plant invasions in the tropics may increase in the future due to the introduction of shade-tolerant exotic species in forest plantations (Fine 2002). Mountain forest ecosystems are isolated from surrounding habitats by their specific climate. These ecosystem barriers make highland ecosystems less likely to be invaded than lowland areas, but also vulnerable due to anthropogenic disturbances (Kašák et al. 2015; Martin and Bellingham 2016). ‘ Sleeper weeds ’ that are already introduced and naturalized in tropical environments are potential invasive species and will likely become invaders once the supporting biotic and abiotic factors occur (Duursma et al. 2013) due to high disturbance rates in these tropical forests. Naturalized alien species, which are defined as “alien species that reproduce consistently (cf. casual alien plants) and sustain populations over many life cycles without direct intervention by humans” (Richardson et al. 2000), are potential invaders into tropical forests. Human intervention or impact through

socioeconomic activities is also believed to be one of biological invasion causes, termed ‘invasion debt’ (Essl et al. 2011). Lastly, the time needed for exotic species to become invasive (lag time) may be shorter for tropical ecosystems relative to sub-tropical (Daehler 2009).

Morphological, anatomical, biochemical, physiological or phenological features (Violle et al. 2007) are important factors for invasion ecology and invasibility. Several traits such as specific leaf area (SLA) and seed mass are useful proxies (Drenovsky et al. 2012; Junaedi et al. 2021) to predict the occurrence of plant invasion (Salguero - Gómez 2016, but see Funk et al. 2021 and Catford et al. 2019). For instance, Cornwell and Ackerly (2010) concluded that the local scale abundance of native coastal woody plants correlates with SLA, maximum plant height, and wood density. Leaf traits are useful for invasive species (and native species) management and studies because leaf traits are relatively easy to measure and are informative proxies for invasion process parameters. SLA is a reliable indicator to distinguish invasive exotics from non-invasive exotic plants (van Kleunen et al. 2010). SLA also correlates with plant growth rate (Gibert et al. 2016). Leaf thickness of native species is significantly different from introduced species under similar light irradiance (Osunkoya et al. 2014). Thus, leaf traits indicate the physiological and anatomical aspects of exotic invasive plant species.

While leaf traits are hypothesized as an important variable explaining plant invasion, environmental factors such as elevation may predict the distribution of invasive species (Becker et al. 2005; Ahmad et al. 2018; Arévalo et al. 2005). Alexander et al. (2011) detected a global pattern of exotic plant species decrease along elevational gradient at mountain forests. However, this pattern is debatable (Pysek et al. 2011). Therefore, disentangling the effect of leaf traits and elevation is needed to explain the abundance of the invasive species.

In this study we explored the influence of leaf traits and elevation on the number of individuals and richness of exotic plant species. Specifically, we tested the following hypotheses:

(i) Leaf traits and elevation influence the number of individuals of naturalized species; the thicker the leaf thickness the less the individual numbers of the exotic species. The higher the altitude the less the individual numbers of the exotic species; and

(ii) Leaf traits and elevation influence the abundance weighted richness of naturalized species; the thicker the leaf thickness the less the exotic species richness. The higher the altitude the less the exotic species richness.

The study aimed to examine whether the number of individuals and abundance weighted richness of exotic plant species along the hiking-trail of the mountain forest area correlated with leaf traits and environmental factors. We posed two questions in this study. Firstly, whether the analyzed variables explained the number of individuals of naturalized alien plant species; secondly, whether these variables explained the abundance-weighted species richness (AWR) of the same naturalized alien species. We constructed and analyzed a multiple linear regression model of the number of individuals of naturalized alien plant species to answer the first question and an analogous model of AWR to answer the second question. Information on the correlation of exotic species traits and abundance in mountain forests will be useful for invasive species risk assessment to support exotic species management. This information may shed some light on invasion patterns in tropical forests. We conducted these studies at the Cibodas Biosphere Reserve (CBR), which is one out of eight Indonesian biosphere reserves. Invasive exotic species management in this CBR area could support native biodiversity conservation because CBR has important and strategic values for Indonesian biodiversity conservation due to the endemic and endangered species contained in this area.

2 Materials and Methods

2.1 Study area and plot design

This study was conducted within the core area (the conserved forested area) of the Cibodas Biosphere Reserve (CBR). Cibodas Biosphere Reserve is the oldest Indonesian biosphere established in 1977, and contains numerous endemic and rare species (Man and Biosphere Indonesia 2011). This biosphere reserve core area constitutes the Mount Gede-Pangrango National Park (MGPNP) and is considered an important national and global conservation area. The national park covers an area of 22,851 ha and is located in the regions of Cianjur, Sukabumi, and Bogor in West Java (Indonesia). According to the

updated Koppen-Geiger climate classification (Kottek et al. 2006), the national park belongs to the Type Af (precipitation ≥ 60 mm) that refers to tropical humid rainforest climate. The annual mean temperature in MGPNP decreases gradually from 18°C at 1,400 m asl. to a minimum of 0°C at mountain summits at 3,019 m asl. and 2,962 m asl. The annual rainfall ranges from 3,000 to 4,200 mm yr⁻¹ with most of the precipitation in the wet season between December and March. The forest is classified as a moist montane tropical forest (van Steenis et al. 1972). The area hosts about 120 different tree species (DBH >10 cm), with the four most abundant ones (*Schima wallichii*, *Altingia excelsa*, *Vaccinium varingiaefolium*, and *Castanopsis acuminatissima*) accounting for 57% of the total biomass (Rozak et al. 2017).

We conducted sampling in five locations, at five different slopes of MGPNP: Bodogol (S6°46' 25.50", E106°50'30.65") at 736-918 m asl., Tapos (S 6°72'099", E106°88'826") at 748-1195 m asl., Cisarua (S6°73'422", E106°91'218") at 960-1256 m asl., Selabintana (S6°50'03.50", E106°58'11.20") at 1460-1537 m asl., and Tegalega (S 6°46'25.50" E 106°50'30.65") at 1251-1266 m asl. (Fig. 1). For all five locations, we sampled four to six plots placed along a transect defined by a hiking trail. During the sampling data collection, we started the sampling transect from the forest exterior and ended the transect in the forest interior. The minimum distance between each plot in a transect was 100 meters. The size of each plot was 10 meters wide by 50 meters long. In total, 24 plots covering an area of 12,000 m² (1.2 ha) were sampled.

We did not conduct sampling at the same altitude for all five locations for two main reasons. First, we aimed to examine the habitat elevation effect on exotic plant species abundance. Second, the land use contexts from one location to another were mostly different at the same elevation. For instance, at elevation 800 m asl., there is a forest ecosystem that exists in Bodogol, but we only found villages and agriculture land at the same elevation at Selabintana. Therefore, the starting point of the first plot for each trail was varied as there were some areas that at lower elevations had villages and agricultural lands.

We also conducted a species-area curve analysis to examine whether our sampling size was representative. The species-area curve from our analysis showed that the sampling number is representative because the curve shape that reached a plateau beyond 20 plots (Appendix 1).

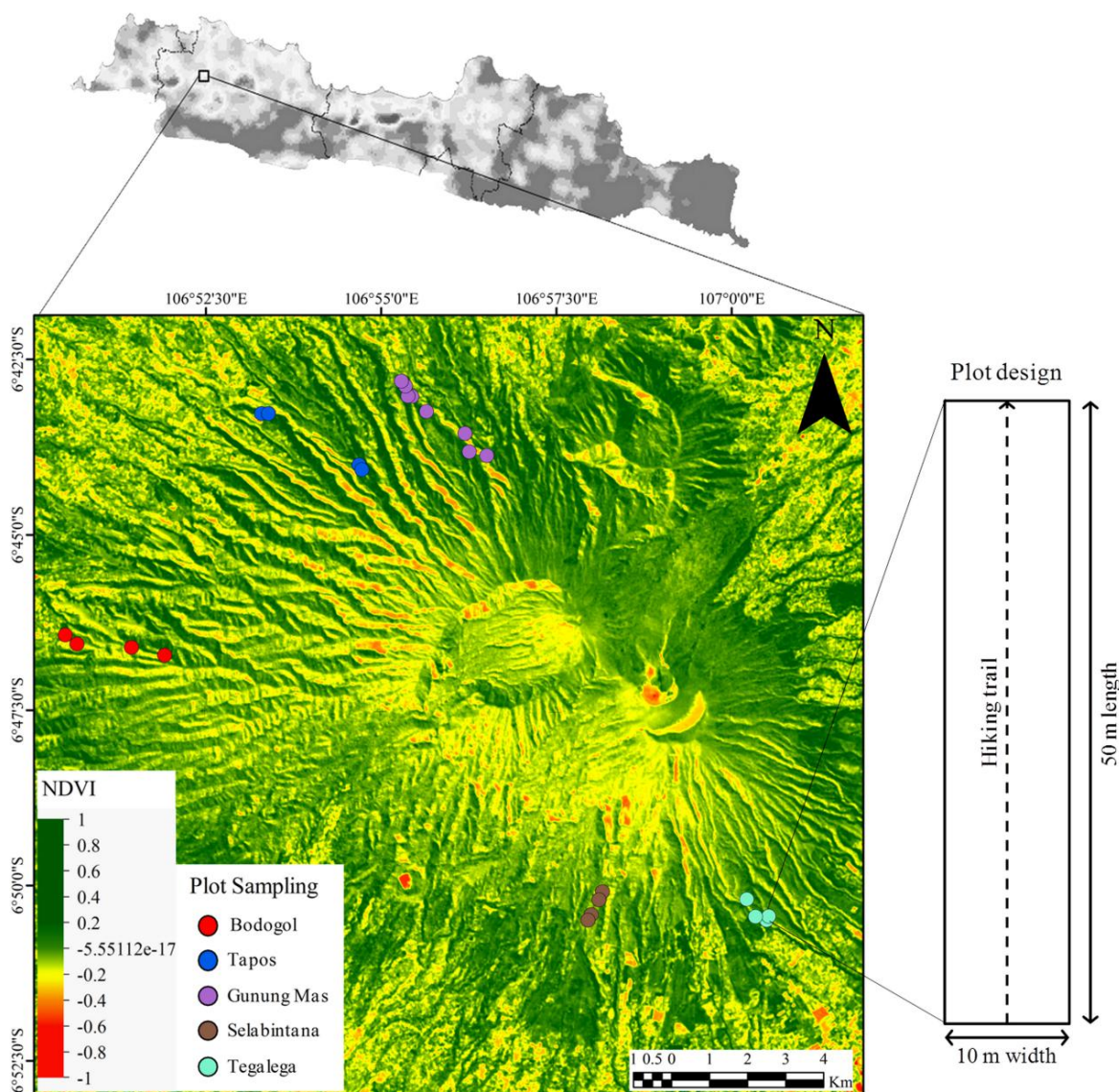


Fig. 1 Five sampling locations and plot design of the study in Mount Gede Pangrango National Park: Bodogol, Tapos, Cisarua, Selabintana, and Tegalega and its relative position within Java Island, Indonesia. Each plot covered an area of 500 m². Altitude range = 736 - 1537 m asl. The figure also describes the NDVI map (based on Landsat 8 OLI, date July 18th, 2018, from <https://earthexplorer.usgs.gov/>, accessed on March 29th, 2019).

2.2 Data collection and measurement

We counted the number of individuals of each exotic species found within the plot. In each plot, we collected leaf samples of each exotic species to calculate specific leaf area (SLA) and leaf thickness. We collected leaf samples near the end of the branches, exposed to maximum light intensity, and with varying height depending on the life form of the naturalized alien plant species (Perez-Harguindeguy et al. 2013). We recorded the latitude and longitude as well as the altitude of each plot using a GPS device.

The normalized difference vegetation index (NDVI) and distance to the forest edge from the nearest border of the plot were calculated based on the position of each plot. A total of five explanatory variables (Table 1) were used to explain two dependent variables: the number of detected naturalized alien individuals and the abundance-weighted richness of naturalized alien species.

SLA is calculated as the ratio between leaf area (mm²) and dry leaf mass (mg). We collected five to ten leaves for each exotic species found in at least one plot. We measured SLA and leaf thickness from all leaves following the protocol from Perez-

Table 1 The five explanatory continuous variables used in this study with the units, median, minimum value, and maximum value across the plots. This study did not include categorical or ordinal variables. Sample size = 104 measurements from 24 plots.

| Variables | Units | Median | Min. | Max. |
|-----------------------------|----------------------------------|--------|------|--------|
| Specific leaf area | mm ² mg ⁻¹ | 44.55 | 2.56 | 287.19 |
| Leaf thickness | mm | 18.11 | 0.29 | 37.46 |
| NDVI | - | 0.40 | 0.31 | 0.48 |
| Habitat elevation | m | 1147 | 736 | 1537 |
| Distance to the forest edge | m | 200 | 2.0 | 2660 |

Harguindeguy et al. (2013). Leaf thickness was measured using a Vernier Mitutoyo caliper. For SLA measurement, leaves were stored in a plastic bag when collected from the field then photographed for capturing leaf image and area data, and dried and weighed to collect dry leaf mass data. We measured the dry leaf mass in groups of 5-10 dry leaves of the same species.

The NDVI value of our study site was extracted from the Landsat 8 OLI (8th July 2018) and calculated using the Eq. (1):

$$NDVI = \frac{NIR-Red}{NIR+Red} \quad (1)$$

where NIR is a reflection in the near-infrared band ($\lambda \sim 0.8 \mu m$) and Red is a reflection in the red band ($\lambda \sim 0.6 \mu m$) regions of the spectrum, respectively, reflected by the vegetation and captured by the sensor of the satellite. The formula is based on the fact that chlorophyll absorbs Red whereas the mesophyll leaf structure scatters NIR. NDVI values thus range from -1 to +1, where negative values correspond to an absence of vegetation (Myneni et al. 1995). To minimize the atmospheric effects on our NDVI calculation, we selected a cloudless image for our study site, and therefore did not conduct atmospheric correction.

2.3 Statistical model and analysis

2.3.1 Model of number of individuals per species

We modelled the linear correlation between the number of individuals per naturalized alien plant species per plot and the species' leaf traits and habitat data. The number of individuals per species per plot refers to the number of individuals detected during plot sampling. Based on our sampling result, the number of individuals may reach more than 400

individuals in a plot (Appendix 2).

Since the observed data were not normally distributed and varied in their ranges (Table 1), we standardized all variables (SV). We standardized the value (Gelman 2008) by subtracting it with the mean (M) and dividing it by the standard deviations value (SD). The SV was calculated by the Eq. (2):

$$SV = \frac{(value - M)}{SD} \quad (2)$$

where SD is calculated as Eq. (3):

$$SD = \sqrt{\frac{\sum (value - M)^2}{N - 1}} \quad (3)$$

Thus, we conduct data analysis based on the following model (Eq. (4)):

$$S = \beta_0 + \beta_1 SV_1 + \beta_2 SV_2 + \beta_3 SV_3 + \beta_4 SV_4 + \beta_5 SV_5 + error \quad (4)$$

where *S* refers to the observed number of individuals of a naturalized alien species in a given plot. The *SV*₁, *SV*₂, *SV*₃, *SV*₄, and *SV*₅ refer to a standardized specific leaf area for the species (SLA), standardized leaf thickness for the species, habitat elevation for the plot, distance to forest edge of naturalized alien species for the plot, and NDVI for the plot. We also normalized the data by using a log-transformation and conducted Pearson correlation tests to check for possible collinearity issues. All the models were analyzed using Bayesian multiple regression, conducted in R (R Core Team 2018) using package “rjags” to call JAGS from R and Rstudio (Plummer 2019).

2.3.2 Model of abundance-weighted richness (AWR)

For each plot *i*, an abundance-weighted richness (AWR_{*i*}) was calculated as the product of the species number of exotic species in plot *i* (*x_i*) and the number of exotic individuals in plot *i* (*y_i*) relative to the total number of exotic individuals across all plots (*z*). Hence, for each plot, the AWR was calculated by the Eq. (5):

$$AWR_i = \frac{x_i \times y_i}{z} \quad (5)$$

A linear mixed model for AWR was developed to test for the effect of SLA (*X*₁), leaf thickness (*X*₂), the altitude of the plot (*X*₃), distance to the forest edge (*X*₄) from the plot, and NDVI in the plot (*X*₅). Thus, the full model of AWR (*Y*) was modeled by the Eq. (6):

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_5 + u + error \quad (6)$$

Table 2 Exotic plant species found in 24 sampling plots at five trails/locations in Mount Gede-Pangrango National Park. Surveys conducted on an elevation between 736-1537 m asl. Symbol “+” represents the presence of corresponding species in the corresponding location: (+) exotic species detected in one plot, (++) detected in two plots, (+++) detected in three plots, (++++) detected in four plots. Origin refers to the natural distribution of the species (<http://www.plantsoftheworldonline.org/>). (No.= Number of detected individuals)

| Species name | Bodogol | Tapos | Cisarua | Tegalega | Selabintana | No. | Origin |
|-------------------------------------|---------|-------|---------|----------|-------------|------|-------------------------------------------------------------------------------|
| <i>Ageratum conyzoides</i> | | + | | | | 6 | Mexico |
| <i>Ageratina riparia</i> | | + | + | +++ | ++ | 678 | Mexico |
| <i>Austroeupatorium inulifolium</i> | ++ | ++ | +++ | | + | 247 | Panama to South Tropical America, Trinidad |
| <i>Borreria cf alata</i> | + | | | | | 5 | Colombia to North South America and West Brazil |
| <i>Brugmansia x candida</i> | | | +++ | | + | 77 | South Colombia to Ecuador |
| <i>Calliandra calothyrsus</i> | ++ | + | ++++ | + | | 1047 | South Mexico to Central America |
| <i>Carex cf baccans</i> | | | | | +++ | 16 | Tropical & Subtropical Asia |
| <i>Cestrum aurantiacum</i> | | | | + | | 14 | Mexico to Venezuela |
| <i>Cinchona pubescens</i> | | + | + | | + | 227 | Costa Rica to West South America |
| <i>Cinchona succirubra</i> | | | | + | | 10 | Costa Rica to West South America |
| <i>Clidemia hirta</i> | ++++ | +++ | ++++ | ++++ | ++++ | 1136 | Mexico to Tropical America |
| <i>Clibadium surinamense</i> | | ++ | | | | 55 | Tropical America |
| <i>Costus cf speciosus</i> | | ++ | | | | 25 | Tropical & Subtropical Asia and North East Queensland |
| <i>Dracaena cf angustifolia</i> | | | + | | | 40 | Tropical & Subtropical Asia to North Australia |
| <i>Erechtites valerianifolius</i> | | + | | | | 13 | Mexico to Tropical America |
| <i>Erechtites cf hieracifolia</i> | + | | | | | 12 | Tropical America |
| <i>Eupatorium cf odoratum</i> | ++ | | | | | 66 | Tropical & Subtropical America |
| <i>Hedyotis philippensis</i> | | ++ | | | | 91 | Hainan, Philippines |
| <i>Hydrocotyle sibthorpioides</i> | | | + | | | 9 | New Zealand to Kermadec Islands |
| <i>Justicia cf tinctoria</i> | | + | | | | 5 | South India, Sri Lanka, Andaman Islands to Nicobar Islands, Hainan to Vietnam |
| <i>Lophatherum gracile</i> | | ++ | | | | 287 | South China to Japan and Tropical Asia, North Queensland |
| <i>Maesopsis eminii</i> | +++ | ++ | +++ | | | 151 | Liberia to South Sudan and Zamb |
| <i>Melastoma malabathricum</i> | | + | | | + | 14 | Seychelles, Tropical & Subtropical Asia to North & East Australia |
| <i>Oxalis barrelieri</i> | | + | | | | 13 | Tropical America |
| <i>Piper aduncum</i> | | ++ | | | | 711 | Mexico to Tropical America. |
| <i>Pinus merkusii</i> | + | | ++ | | | 12 | Sumatera, Philippines |
| <i>Solanum torvum</i> | ++ | + | + | | | 20 | Mexico to North South America, Caribbean, East Brazil |
| <i>Spilanthes cf paniculata</i> | + | | | | | 10 | China (Guangdong, Guangxi, Yunnan), Taiwan, Laccadives to Queensland |
| <i>Stachytarpheta jamaicensis</i> | + | + | | | | 112 | South East U.S.A. to Tropical America |
| <i>Strobilanthes hamiltoniana</i> | | | | ++ | | 121 | East Nepal to South East Tibet and North Thailand |
| <i>Strobilanthes cf cernua</i> | | | + | | | 20 | Sumatera to Bali |
| <i>Strobilanthes cf paniculata</i> | | + | | | | 19 | Indo-China to West Malesia |
| <i>Strophacanthus dichotomus</i> | | | | + | | 6 | South Malesia |
| <i>Synedrella nodiflora</i> | + | | | | | 5 | Tropical & Subtropical America |
| <i>Wedelia biflora</i> | + | | | | | 27 | Mozambique to KwaZulu-Natal, West Indian Ocean to Pacific |
| Total | | | | | | 5307 | |

where β is the coefficient of the predictor, and u is a random effect for plot. Plot locations were considered as a random factor to minimize spatial auto-correlation effect in the model. SLA, leaf thickness, altitude, and distance to the forest edge were not normally distributed ($p < 0.05$, Shapiro-Wilk Normality Test). To fulfill normality assumptions as well as to avoid heteroscedasticity of the residuals, these variables were log-transformed. We also performed Pearson correlation tests to check the correlation between analyzed variables. All analyses in the plot level were performed using the following packages: “lme4” to fit linear mixed models (Bates et al. 2015), “glmulti” to predict the best fit model based on the lowest Akaike Information Criterion with correction (AICc) and to calculate the relative importance value for each fixed factor (Calcagno 2010), “MuMIn” to extract marginal (i.e., the proportion of variance explained by fixed factor) and conditional (the proportion of variance explained by a fixed and random factors) R^2 of the model (Barton 2009), and “car” to analyze significance in differences between fixed factors (Fox and Weisberg 2019).

3 Results

We found a total of 5307 individuals that belongs to 35 exotics species in 24 sampling plots (Table 2). One species, i.e., *Clidemia hirta*, was found in all locations. The majority of the species (24 out of 35) were found in only one sampling plot.

3.1 Model of number of individuals

We did not detect any significant effect of explanatory variables on the number of individuals of naturalized alien species (Fig. 2, Appendix 3). Apart from leaf thickness, we found insignificant negative correlations between explanatory variables with the number of naturalized exotic plant species individuals.

3.2 Model of abundance-weighted richness

The full model explained the AWR with marginal and conditional R^2 of 70% and 77%, respectively (Table 3). Leaf thickness and altitude were positively and negatively correlated with plot-level AWR, respectively. Those two variables showed high relative importance value (>0.8 , Appendix 4) and always

Table 3 The coefficient (β), standard errors (SE), degree of freedom (df), t-value, and p-value (P) of the full model (Eq. 6). Detected correlations are marked by asterisks (*).

| Predictor | β | SE | df | t-value | P |
|-----------------|---------|-------|-------|---------|--------|
| Intercept | 18.89 | 10.49 | 7.34 | 1.80 | 0.113 |
| SLA | 0.81 | 0.54 | 17.74 | 1.50 | 0.152 |
| Leaf thickness* | 2.21 | 0.49 | 17.33 | 4.48 | <0.001 |
| Altitude* | -8.74 | 3.30 | 6.26 | -2.65 | 0.037 |
| Distance | -0.14 | 0.43 | 17.66 | -0.34 | 0.740 |
| NDVI | 3.90 | 5.29 | 16.96 | 0.74 | 0.472 |

appeared in the best five models of AWR (Appendix 5). We did not detect any significant effect of SLA, distance to the forest edge, or NDVI to the plot-level AWR.

4 Discussion

Our study investigated the correlation of leaf traits and environmental factors with the number of individual and richness of naturalized alien species in a mountain region of MGPNP. We found that the richness of naturalized alien species was significantly influenced by those two variables, leaf thickness and altitude (Table 3). However, we did not detect any influence of the tested variables on the number of individuals of naturalized alien species (Fig. 2). Our hypothesis that altitude and leaf traits (leaf thickness) influence the naturalized alien species was thus supported only at the context of richness (AWR), but not for number of individuals (Fig. 2).

4.1 Leaf thickness and altitude affect the abundance-weighted richness (AWR) of naturalized alien species

We found leaf thickness and altitude significantly affect the richness of the exotic species in MGPNP (Table 3). The fact that leaf thickness and altitude correlate with AWR provides two insights. Firstly, the light may be a prominent abiotic factor for exotic species to establish and become dominant in native tropical rainforests. In this plot-level model, leaf thickness positively correlated with AWR, meaning that thicker leaves tend to support exotic species development and growth to gain optimum abundance. Thicker leaves indicate greater exposure of leaves to sunlight (Perez-Harguindeguy et al. 2013). Thus, the canopy gaps that provide abundant light resources in

a tropical forest may positively correlate with AWR at plot-level.

Secondly, this richness model shows that the higher altitude area of mountain forests is colonized by less exotic plant species. The traits of these exotic species may limit their abundance at high altitudes. The elevational gradient of invasive species distribution in the mountain ecosystems is also confirmed by other studies (Arévalo et al. 2005; Becker et al. 2005; Ahmad et al. 2018). This negative elevation effect on exotic species richness may be an indication of high-altitude abiotic factors as the limitation for exotic species to become developed and abundant. For instance, the lower air temperature at higher elevation may not be suitable for these exotic species' habitat preferences. However, dispersal pathways may be more crucial than abiotic extreme conditions for invasion resistance within high-altitude plant ecosystems (Alexander et al. 2009).

4.2 Undetected effect of leaf traits and abiotic (habitat) factors on the number of individuals of naturalized alien species

Despite the suggested correlation between the abundance of exotic species and their traits (Cornwell and Ackerly 2010), we found no effect of five explanatory variables on the number of individuals of naturalized alien species (Fig. 2). The undetected effects of these abundance-trait correlations were surprising. These findings may be due to the exclusion of the life stages of the samples. We did not consider the life stages of measured individuals for leaf trait measurements. Leaf traits may have fluctuated, and the range of intraspecific variation may be driven by life-stages (Spasojevic et al. 2014; Funk et al. 2021). The plasticity of SLA of tropical forest plant species is relatively large (Rozendaal et al. 2006) and these variations may not be captured in our study.

Moreover, the facts that naturalized alien species with large number of individuals are having smaller SLA values are quite interesting since large SLA values are associated with potential invasiveness (Van Kleunen et al. 2010). This finding may indicate that larger SLA values are only associated with the early stage of invasion (naturalization), but not for the later invasion stages. Catford et al. (2019) stated that SLA is highly correlated with the abundance of exotic species at early plant invasion stages, but not for further invasion processes.

Furthermore, the naturalized alien species with

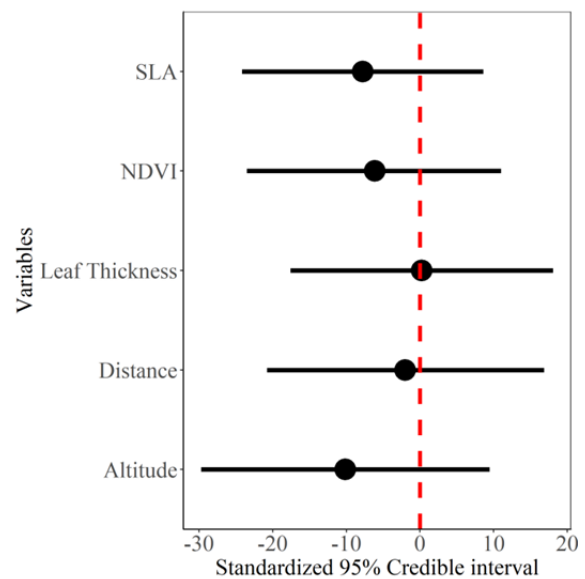


Fig. 2 Variable coefficient results of the analysis results of the number of individual model (Eq. 4). Detected effects are indicated by a 95% confidence interval (horizontal lines) that does not include zero (red dashed lines). We did not detect any significant effect of explanatory variables of the number of naturalized alien individuals.

large number of individuals may have a conservative adaptation (invest more energy into biomass than into fast growing rate) due to their life strategy. The conservative strategy of these species may be indicated by their relatively low SLA value given the fertile soil conditions of the invaded habitat (Maracahipes et al. 2018) and low SLA is a common plant adaptation in tropical forest ecosystem (Tian et al. 2016). However, these hypotheses still need to be tested since we did not consider soil fertility aspects in this study. We suggest including this soil edaphic factor in further study to answer whether these naturalized alien species with large number of individuals have a conservative (aim for higher biomass) or acquisitive (aim for faster growth rate) adaptation strategy.

4.3 Limitations of the study

There are several limitations within this study. First, we did not collect light intensity or canopy cover measurements as a proxy for light. Light is an important abiotic factor for plant invasion in tropical forests (Martin et al. 2009). Even though we collected NDVI as a proxy for canopy closure, we did not consider the possibility that wide leaf color ranges may bias the estimation of canopy closure based on

NDVI. However, NDVI was considered an unimportant variable in both the number of individuals model and the richness model.

Second, we also did not consider the edaphic factors. Nutrition factors may contribute to exotic plant abundance. The ratio of N and P correlates with the growth and competitive dominance of invasive plant species (Zhang et al. 2017). However, we focused on leaf traits (SLA and leaf thickness) that could be utilized as a proxy for plant-environment relation indicators (Cornwell and Ackerly 2010; Spasojevic et al. 2014) and altitude, which is a simple proxy and an important factor for exotic plant species distribution and patterns in mountainous ecosystem contexts (Alexander et al. 2009; Pyšek et al. 2011).

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Authors' Contribution

All authors were equally contributed to the field data collection. DIJ and AHR were conducted analysis and interpretation of data. DIJ conducted abundance model analysis. AHR conducted richness model analysis. IWH conducted NDVI data calculation and

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5 Conclusion

This study showed that leaf thickness and elevation are positively and negatively correlated with exotic plant species richness, respectively. Consequently, these traits are useful parameters to be used in the exotic plant species management in the mountain forests ecosystem. For the specific context of this study site (Mount Gede-Pangrango), the management of exotic plant species should be prioritized and focused in a forest area with gaps and located at a lower elevation. Further study needed to include other abiotic factors such as light and edaphic (soil) factors to model the abundance of exotic plant species in the tropical mountain forests.

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created map data. DIJ, ZM, MZ, IWH, and AHR were equally contributed to the methods design. DIJ, AHR, MZ, IWH, and ME were equally contributed to the manuscript writing. DIJ, AHR, IWH, and ME were equally contributed as main authors.

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