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Invasion hotspots in wilderness zones of tropical national parks

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Abstract. Invasive alien plant species increasingly threaten the integrity of forest ecosystems in protected areas, particularly within poorly studied wilderness zones of tropical national parks. The aim of this study was to assess the spatial distribution and invasion intensity of invasive alien plant species in the wilderness zone of Gunung Ciremai National Park, West Java, Indonesia. During the wet season, a comprehensive geographical investigation was conducted using twelve systematically established plots (20 × 20 m) with nested subplots representing different growth stages. A total of 18 invasive alien plant species belonging to nine families were recorded. Hierarchical cluster analysis identified three statistically distinct invasion intensity zones: a moderately invaded zone (67% of plots) dominated by Panicum maximum and Isachne globosa; a highly invaded zone (25% of plots) characterised by strong dominance of the woody legume Calliandra calothyrsus; and a low-invasion zone (8% of plots) with minimal establishment. Between-cluster Bray-Curtis dissimilarity (0.72 ± 0.18) exceeded within-cluster values (0.52-0.65), indicating pronounced compositional differentiation. A corridor-based invasion pattern was supported by a significant decline in invasion intensity with increasing

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distance from trails ($R^2 = 0.78$, $p < 0.001$). The study provided the first quantitative spatial assessment of invasive plant distribution in wilderness zones of Indonesian protected areas and demonstrated the value of multivariate analyses for identifying invasion hotspots and informing targeted management strategies

Keywords: biological invasion; Bray-Curtis dissimilarity; cluster analysis; protected areas; spatial patterns

Introduction

Invasive alien plant species (IAPS) represent a growing threat to forest ecosystems worldwide, undermining biodiversity, altering community structure, and challenging the effectiveness of conservation efforts in protected areas. Although national parks are established to safeguard ecological integrity, human activities such as recreation, trail development, and landscape modification can facilitate the introduction and spread of invasive species even in zones designated for strict protection. Wilderness areas, often perceived as relatively undisturbed, remain particularly vulnerable due to limited monitoring and the assumption of natural resistance to biological invasions. As a result, the spatial dynamics and drivers of invasive plant establishment in these areas remain insufficiently understood, especially within tropical forest ecosystems.

K. Utkhamthiang *et al*. (2025) assessed the severity and spatial distribution of invasive plant species along a nature trail within the Doi Chiang Dao Biosphere Reserve in northern Thailand. Their study demonstrated that invasion intensity increased in proximity to recreational trails, highlighting the role of anthropogenic disturbance as a key driver of invasive species spread in protected forest ecosystems. The authors emphasised the importance of trail-based monitoring for early detection and management of biological invasions in conservation areas. Developments in spatial ecology have enhanced the understanding of invasion dynamics in protected forests. S.E.N. Pang *et al.* (2023) demonstrated that clustering analysis can reveal spatially associated species patterns and invasion hotspots that are not captured by traditional diversity indices. Likewise, M. Wang *et al.* (2024) showed that functional traits and phylogenetic relationships jointly shape species distributions through environmental filtering and dispersal limitation. Together, these studies suggested that invasion patterns in wilderness zones result from complex interactions between anthropogenic disturbance and natural ecological processes rather than from a single driver.

In their review, H.D. Flickinger & J.S. Dukes (2024) compared theoretical approaches to invasion ecology and the shifting of species ranges induced by climate change. They provided an overview of existing theories that combine these two aspects, highlighting the importance of considering climate change as a key driver for understanding invasion mechanisms. The paper was significant for studies addressing invasive species, as it bridged the concepts of climate change and invasion dynamics, which are crucial for managing forest ecosystems in response to emerging threats. Climate change adds a layer of vulnerability to montane protected areas. A. Poudel *et al.* (2024) predicted that rising temperatures will allow highly invasive species to colonise higher elevations previously constrained by climate. Advances in invasion detection methodologies have improved spatial assessment capabilities. R. Sengupta & S.S. Dash (2024) demonstrated that species distribution modelling can effectively identify invasion hotspots and support targeted monitoring efforts in data-limited regions. P.B. Rakgoale & S.N. Ngetar (2024) further showed that integrating remote sensing with machine learning and deep learning substantially improves the detection accuracy of invasive species at landscape scales. I. Kim *et al.* (2025) emphasised that native forest structure and species diversity strongly influence invasive plant richness and invasion resistance. Despite these methodological advances, ground-based field data remain indispensable, particularly in remote wilderness zones where satellite-based detection is constrained by dense canopy cover and complex forest structure.

J. Chen *et al.* (2024) explored the application of ensemble learning algorithms to improve the performance of forest age prediction models using satellite remote sensing data. They demonstrated that by combining multiple learning algorithms, it is possible to enhance the accuracy of age predictions for forest ecosystems, which is crucial for forest management and monitoring. The study effectively highlighted the potential of remote sensing data and machine learning techniques in ecological research, specifically in predicting forest parameters, such as age, which is directly relevant to understanding forest dynamics and ecosystem health. P.E. Hulme (2024) identified international tourists as significant biosecurity pathways into national parks, emphasising that recreation intensity and visitor movement patterns are critical factors influencing invasion dynamics alongside physical infrastructure. Despite growing research interest, substantial knowledge gaps persist. Most invasion studies focus on easily accessible areas, leaving wilderness zones largely understudied, particularly in tropical Southeast Asia. Few investigations apply multivariate spatial analyses to test corridor-invasion hypotheses using fine-scale data from strictly protected areas. L. Petri & I. Ibáñez (2025) demonstrated that effective invasive species management can facilitate native plant recovery, underscoring the importance of understanding current invasion patterns to inform restoration strategies. These gaps highlight the need for integrated spatial assessments combining field surveys, cluster analysis, and distance-based modelling in tropical montane wilderness zones.

The aim of this study was to assess the spatial distribution, invasion intensity, and trail-related drivers of invasive alien plant species in the wilderness zone of Gunung Ciremai National Park (GCNP), Indonesia. The objectives were to: (1) document species diversity across growth stages; (2) detect spatial heterogeneity using cluster analysis; and (3) quantify relationships between invasion patterns and disturbance gradients. Invasion intensity was hypothesised to decline with increasing distance from trails, and clustering revealed successional zones.

Materials and Methods

Study site and environmental context. Research was conducted in GCNP wilderness zone, West Java, Indonesia (6°46’57”-6°58’57” S, 108°19’18”-108°29’30” E). GCNP is a 15,500-ha mountain forest ecosystem on Java’s highest single volcano (3,078 masl). The study area altitude ranged from 928 to 1,040 m with slopes of 30-65% (Fig. 1). The average annual temperature ranges from 18 to 25°C, with rainfall distributed across two seasons: a wet season (November to April) and a dry season (May to October). Dominant native vegetation includes *Castanopsis argentea*, *Schima wallichii*, and *Altingia excelsa* (TNGunungCiremai, n.d.).

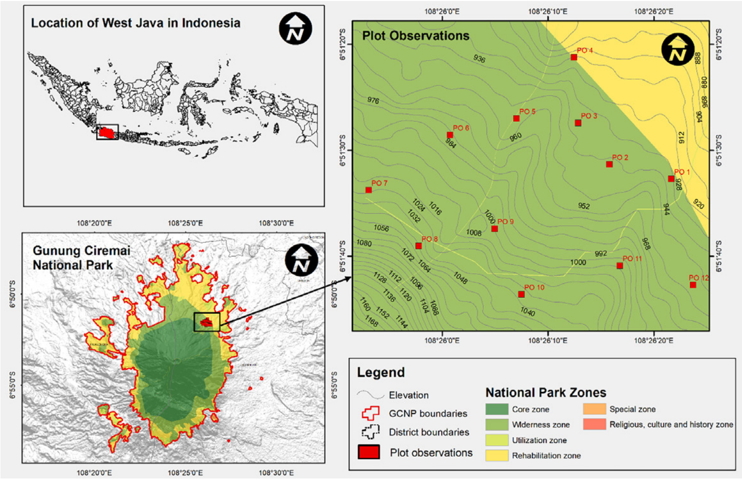

Figure 1. Map of research location in the wilderness zone of GCNP, West Java, Indonesia
Source: Tanah Air Indonesia (n.d.)

A maintained trail from the utilisation zone boundary provides access to the wilderness zone, potentially establishing invasion corridors through propagule dispersal and trail-edge disturbance (Barros *et al.*, 2025). *Calliandra calothyrsus* plantings in adjacent agroforestry systems (<500 m distant) provide propagule sources. Southwest-northeast winds during the wet season may facilitate seed dispersal into the wilderness interior.

Field sampling and data collection. To counteract the seasonal bias where dry-season sampling underestimates species richness by 30-40%, surveys were conducted during the wet season (November-December 2024), when germination peaks. Twelve observation plots (20 × 20 m, 0.48 ha total) were systematically established along transects perpendicular to main trails, stratified by elevation and trail distance (0-50 m, 51-100 m, > 100 m) (Fig. 1). Each plot used a nested subplot design: four 2 × 2 m subplots for saplings (1.5-3 m height, diameter < 10 cm), one 1 × 1 m subplot for seedlings (< 1.5 m height), and a whole 20 × 20 m plot for poles (diameter 10-20 cm) and trees (diameter > 20 cm). Environmental variables measured included elevation (GPS), slope (clinometer), canopy cover (spherical densimeter), and distance to trail. All fieldwork was conducted in compliance with ethical standards for biodiversity research and in accordance with the principles of the Convention on Biological Diversity (1992).

Data analysis. To comprehensively characterise species diversity and spatial structure of invasive alien plant communities, a set of complementary diversity and distribution indices was applied. Species diversity was quantified using the Shannon-Wiener index (H'; Eq. 1), where pi represents the proportion of individuals of species *i* relative to the total number of individuals (N); Simpson's dominance index (C; Eq. 2), calculated as the sum of squared species proportions (Σpi^2); Evenness (EH; Eq. 3), expressed as the ratio of H' to the natural logarithm of species richness ($\ln S$); species richness (R; Eq. 4), defined as the total number of species (S); and Margalef's index (Dmg; Eq. 5), which standardises species richness by sample size using the total number of individuals (N):

$$H' = -\Sigma pi \ln pi, \tag{1}$$

$$C = \Sigma pi^2, \tag{2}$$

$$EH = H'/\ln S, \tag{3}$$

$$R = S, \tag{4}$$

$$Dmg = (S - 1)/\ln N. \tag{5}$$

Spatial distribution patterns were assessed using Morisita's index ($I\delta$; Eq. 6), where q denotes the number of sampling units, x is the number of individuals per sampling unit, Σx^2 is the sum of squared individuals across all units, and N is the total number of individuals:

$$I\delta = q[\Sigma x^2 - N]/[N(N - 1)]. \tag{6}$$

Values of $I\delta < 1$, $= 1$, and > 1 indicate uniform, random, and clumped distributions, respectively. Importance values (IV = RF + RD + RDo) integrated relative frequency (RF), defined as the proportion of sampling units in which a species occurred relative to the total frequency of all species; density (RD), calculated as the number of individuals of a species divided by the total number of individuals across all species; and dominance (RDo), expressed as the contribution of a species to total community dominance, typically based on basal area or canopy cover relative to all species.

Cluster analysis. Hierarchical cluster analysis, using Ward's linkage with Bray-Curtis dissimilarity (Bray & Curtis, 1957; Borcard *et al.*, 2018), was used to reveal spatial invasion patterns in the tropical forest community (Pang *et al.*, 2023). Ward's method minimised within-cluster variation, thereby producing compact clusters suitable for identifying invasion gradients (Borcard *et al.*, 2018). The optimal number of clusters was determined based on dendrogram structure, ecological interpretability, and comparisons of within- and between-cluster dissimilarity. For each cluster, mean abundance, species richness, dominant species composition, and frequency were calculated. Analysis of Similarity (ANOSIM) with 999 permutations was applied to assess the statistical significance of cluster separation. Kruskal-Wallis tests followed by post hoc Dunn's tests were used to examine relationships between clusters and environmental factors, including elevation, slope, canopy cover, and distance from trails. Linear regression analysis was used to evaluate relationships between invasion parameters and distance from trails. All analyses were conducted using R version 4.3.0, with the vegan package for community ecology analyses and the cluster package for hierarchical clustering.

Results and Discussion

Composition and diversity of invasive alien plant species. A total of 18 IAPS from 9 families (421 individuals) were documented across 12 plots (Table 1). Poaceae was most diverse (4 species, 55.6%), followed by Fabaceae (2 species, 30.9%) and Asteraceae (3 species, 4.5%). *Panicum maximum* showed the highest importance value (106.54%), followed by *C. calothyrsus* (92.87%) and *Isachne globosa* (60.02%). These three species comprised 86.5% of the total IAPS abundance, indicating strong dominance.

Table 1. List of invasive alien plant species recorded in the wilderness zone of GCNP

No	Scientific name	Family	Growth stage	Origin	Reference
1	*Ageratina riparia*	Compositae	U	Mexico & the Caribbean (West Indies)	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016)

Table 1, Continued

No	Scientific name	Family	Growth stage	Origin	Reference
2	*Ageratum conyzoides*	Asteraceae	U	Tropical & South America	S. Setyawati *et al.* (2015)
3	*Bidens pilosa*	Asteraceae	U	Southern Africa	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016)
4	*Calliandra calothyrsus*	Fabaceae	Se., Sa., P, T	Central America & Mexico	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016)
5	*Centrosema pubescens*	Fabaceae	U	Central & South America	S. Setyawati *et al.* (2015)
6	*Chromolaena odorata*	Asteraceae	U	Central & South America	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016), Regulation of the Minister of Environment and Forestry of the Republic of Indonesia No. P.16/MENLHK/SETJEN/OTL.0/1/2016 (2016)
7	*Clidemia hirta*	Melastomataceae	U	South America	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016), Regulation of the Minister of Environment and Forestry of the Republic of Indonesia No. P.16/MENLHK/SETJEN/OTL.0/1/2016 (2016)
8	*Cyperus rotundus*	Cyperaceae	U	India / Africa	S. Setyawati *et al.* (2015)
9	*Isachne globosa*	Poaceae	U	South Asia	S. Setyawati *et al.* (2015)
10	*Lantana camara*	Verbenaceae	U	Central America	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016), Regulation of the Minister of Environment and Forestry of the Republic of Indonesia No. P.16/MENLHK/SETJEN/OTL.0/1/2016 (2016)
11	*Melastoma malabathricum*	Melastomataceae	U	Asia	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016)
12	*Mikania micrantha*	Asteraceae	U	Central & South America	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016), Regulation of the Minister of Environment and Forestry of the Republic of Indonesia No. P.16/MENLHK/SETJEN/OTL.0/1/2016 (2016)
13	*Mimosa pudica*	Fabaceae	U	Tropical & South America	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016), Regulation of the Minister of Environment and Forestry of the Republic of Indonesia No. P.16/MENLHK/SETJEN/OTL.0/1/2016 (2016)

Table 1, Continued

No	Scientific name	Family	Growth stage	Origin	Reference
14	*Piper aduncum*	Piperaceae	U, Se., Sa.	South America	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016), Regulation of the Minister of Environment and Forestry of the Republic of Indonesia No. P.16/MENLHK/SETJEN/OTL.0/1/2016 (2016)
15	*Solanum torvum*	Solanaceae	U	Antilles / Caribbean	S. Setyawati *et al.* (2015)
16	*Stachytarpheta jamaicensis*	Verbenaceae	U	Tropical America	S. Setyawati *et al.* (2015), S.S. Tjitrosoedirdjo *et al.* (2016)
17	*Synedrella nodiflora*	Asteraceae	U	Central & South America	S. Setyawati *et al.* (2015)
18	*Panicum maximum*	Poaceae	U	Tropical Africa	S. Setyawati *et al.* (2015), Regulation of the Minister of Environment and Forestry of the Republic of Indonesia No. P.16/MENLHK/SETJEN/OTL.0/1/2016 (2016)

Note: U – Understorey; Se – Seedling; Sa. – Sapling; P – Pole; T – Tree
Source: developed by the authors

Growth stage analysis revealed the following distribution: seedlings (162 individuals, 38.5%), saplings (115, 27.3%), poles (92, 21.9%), and trees (52, 12.4%). *C. calothyrsus* demonstrated successful reproduction across all stages (seedlings 36, saplings 41, poles 28, trees 25), indicating established reproducing populations. Most grass species occurred primarily as seedlings and saplings, suggesting recent colonisation or recruitment limitation. *C. calothyrsus* establishment across all growth stages has critical management implications. Mountain invasions are anticipated to increase as thermal barriers decrease. F. de Vries *et al.* (2023) investigated upward range expansion specifically in tropical mountain systems. They found that invasive plant species exhibited significantly faster altitudinal migration rates (15-30 m per decade) than native species (5-10 m per decade), creating novel community structures at high altitudes. Their study demonstrated that invasive species often possess broader thermal tolerances and greater phenotypic plasticity, enabling them to rapid exploit new, suitable habitats. I. Nasihin *et al.* (2024) applied species distribution modelling to predict the range dynamics of *C. calothyrsus* in the GCNP. They projected continued upward expansion, with a potential increase in suitable habitat of 26.93%. The current findings of established reproductive populations at all growth stages (seedlings to trees) at 900-1,400 m elevation confirm that *C. calothyrsus* has successfully breached historical thermal barriers and established self-sustaining populations in the GCNP mountain wilderness zone, validating the climate-invasion predictions from this study. The findings reveal internal seed sources within the wilderness zone, potentially accelerating invasion through local dispersal. B. Zhang *et al.* (2023) conducted a comparative analysis of dispersal rates between invasive and native plant species across different life forms and ecological contexts. Their study demonstrated that anthropogenic dispersal vectors (human foot traffic, equipment transportation, vehicle movement) facilitate the spread of invasive species at rates 50-100 times faster than natural dispersal mechanisms (wind, animal vectors, gravity). Specifically for invasive herbaceous and woody plants in protected areas, B. Zhang *et al.* documented that trails and recreational infrastructure create dispersal pathways that enable rapid range expansion, with the invasion front advancing 10-50 meters per year along the corridor compared to 1-5 meters per year in undisturbed areas. Their findings emphasise that once invasive species establish a propagule source near a trail, they can rapidly colonise surrounding areas through anthropogenic and natural dispersal, creating accelerating invasion dynamics. The Documentation of a reproductive population of *C. calothyrsus* in Cluster 2 plots (adjacent to the trail) serving as a seed source for Cluster 1 plots (at an intermediate distance) confirms B. Zhang's *et al.* corridor-facilitated invasion model. The presence of an established internal seed source within the wilderness zone, coupled with persistent visitor traffic on the trail, suggests that invasion expansion will continue and potentially increase without targeted interventions to remove the propagule source and disrupt anthropogenic dispersal pathways. Population viability analysis would determine if populations are self-sustaining (requiring containment strategies) or propagule-limited (enabling local eradication through barriers and source control).

Diversity indices showed moderate to high plot diversity (Table 2, 3). The Shannon-Wiener index ranged from 0.82 to 1.98 (mean 1.42 ± 0.35), indicating spatial heterogeneity. Simpson's dominance (0.23-0.67, mean 0.41 ± 0.13) indicated 3-4 species typically dominated each plot. Evenness values (0.51-0.91, mean 0.73 ± 0.12) showed relatively balanced distributions, though some plots displayed single-species dominance. Species richness ranged from 2 to 6 per plot (mean 4.1 ± 1.3).

Table 2. Diversity indices and spatial distribution patterns of invasive alien plant species in the understorey (ground vegetation) of the wilderness zone of GCNP

Species	Density (ind/m^2)	Frequency	H'	C	Distribution (Morisita)
Panicum maximum	45.3	0.83	0.37	0.07	Clumped (1.85)
Isachne globosa	38.7	0.75	0.36	0.04	Clumped (1.92)
Chromolaena odorata	28.5	0.67	0.28	0.05	Clumped (1.65)
Ageratum conyzoides	22.1	0.58	0.24	0.04	Clumped (1.58)
Lantana camara	12.4	0.42	0.12	0.01	Uniform (0.85)
Other species (12 spp.)	53	-	-	-	Variable

Source: developed by the authors

Table 3. Diversity indices and spatial distribution patterns of invasive alien plant species across woody growth stages in the wilderness zone of GCNP

Growth Stage	No. Spp.	Dominant Species	H'	C	Distribution
Seedling (<1.5 m)	2	*C. calothyrsus*	0.23	0.49	Clumped (1.78)
Sapling (1.5-5 cm DBH)	2	*C. calothyrsus*	0.27	0.4	Clumped (1.68)
Pole (5-20 cm DBH)	1	*C. calothyrsus*	0.28	0.46	Clumped (1.55)
Tree (>20 cm DBH)	1	*C. calothyrsus*	0	1	Uniform (0.92)

Note: DBH – diameter at breast height
Source: developed by the authors

Spatial distribution patterns (Morisita's index) demonstrated predominantly clumped distributions: *P. maximum* ($I\delta = 1.84$), *I. globosa* ($I\delta = 2.13$), and *C. calothyrsus* ($I\delta = 3.47$) all showed significant aggregation ($p < 0.05$). Only *Lantana camara* ($I\delta = 1.12$) approached random distribution. Clumped patterns likely reflect vegetative reproduction, limited seed dispersal, and microhabitat preferences, with important implications for targeted control efforts. Wet-season sampling addresses significant temporal bias in Indonesian invasion studies. M. Belayhun *et al.* (2024) conducted comparative wet- and dry-season surveys in Ethiopian protected areas. They documented that wet-season surveys detected 30-40% more invasive species than dry-season inventories, particularly annual forbs and recent colonisers that complete their life cycles during high-rainfall periods. Their findings emphasized the importance of seasonal timing in invasion assessments, as many herbaceous invasive species remain dormant or inconspicuous during dry periods. Wet-season sampling methodology aligns with M. Belayhun's *et al.* recommendations and successfully documented species such as *M. pudica* and grass seedling cohorts during peak rainfall, providing baseline data on species that would likely be overlooked in dry-season inventories. This temporal approach has important implications for control timing, as interventions targeting reproductive stages during wet seasons may be more effective than those targeting dry-season stages. Documentation of *M. pudica* and grass seedling cohorts during high rainfall provides baseline data on species that may be overlooked in dry-season inventories, with implications for control timing.

Spatial invasion patterns and corridor-based invasion dynamics. Hierarchical clustering identified three statistically distinct groups of invasion intensity (Fig. 2; ANOSIM $R = 0.68$, $p = 0.001$), aligning with patterns observed in other tropical forests (Pang *et al.*, 2023). The stated hypothesis was supported by the results, as invasion intensity significantly declined with increasing distance from trails ($R^2 = 0.78$, $p < 0.001$), and hierarchical cluster analysis identified three distinct invasion intensity zones. Between-cluster dissimilarity (mean 0.72 ± 0.18) significantly exceeded within-cluster dissimilarity (Cluster 1: 0.52 ± 0.21; Cluster 2: 0.65 ± 0.31; Kruskal-Wallis $\chi^2 = 18.3$, $p < 0.001$), confirming compositionally distinct zones.

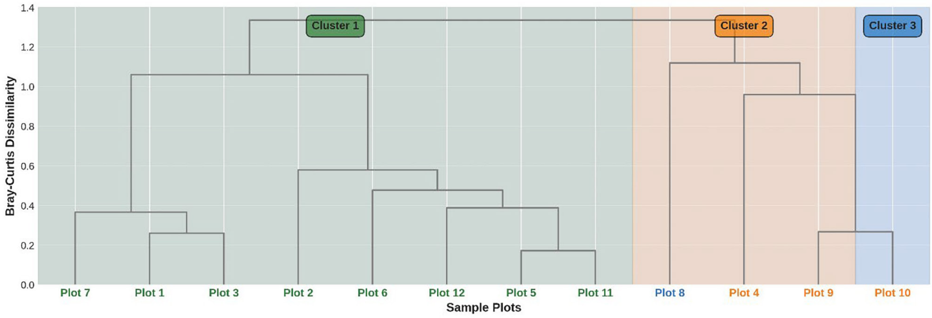

Figure 2. Hierarchical cluster analysis of invasive species composition

Source: developed by the authors

This work provides the first comprehensive spatial analysis of invasive plants within an Indonesian wilderness zone. The hierarchical cluster analysis reveals highly spatially stratified invasion intensity, with three zones differing in species composition, abundance, and functional groups. This spatial heterogeneity has significant management implications: spatial targeting based on invasion intensity mapping can enhance resource allocation, whereas uniform strategies may be ineffective. P. Courtois *et al.* (2023) developed spatially explicit management models for protected areas and demonstrated that stratified management approaches based on invasion intensity zones achieved 3-5 times greater cost-effectiveness than uniform interventions. Their work showed that concentrating resources on high-invasion hotspots, while maintaining surveillance in moderate-invasion zones, prevented both species spread and resource waste. Hierarchical cluster analysis provides precisely this type of spatial stratification, identifying three distinct management zones that enable targeted resource allocation. Compared with P. Courtois's *et al.* framework, Cluster 2 (high invasion, 25% of plots) represents priority intervention zones where immediate control efforts are expected to yield the greatest return. In contrast, Cluster 1 (moderate invasion, 67% of plots) requires sustained monitoring rather than intensive intervention.

Cluster 1: Moderate invasion – grass-dominated assemblages. Eight plots (67%: Plots 1, 2, 3, 5, 6, 7, 11, 12) showed intermediate invasion intensity (37.5 ± 11.5 ind/plot) and the highest diversity (4.6 ± 1.1 species/plot; Figs. 3-5). *P. maximum* (136 individuals, 45.3%) and *I. globosa* (90, 30.0%) predominated, with *C. calothyrsus* contributing 13.0% (39 individuals). Co-dominance without competitive exclusion suggests an early to intermediate stage of invasion. Plots occurred at intermediate trail distances (mean 85 ± 25 m) with moderate canopy openness (45 ± 12%).

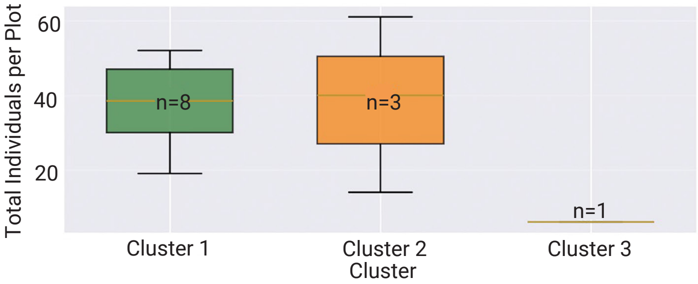

Figure 3. Total abundance

Source: developed by the authors

Figure 4. Species richness

Source: developed by the authors

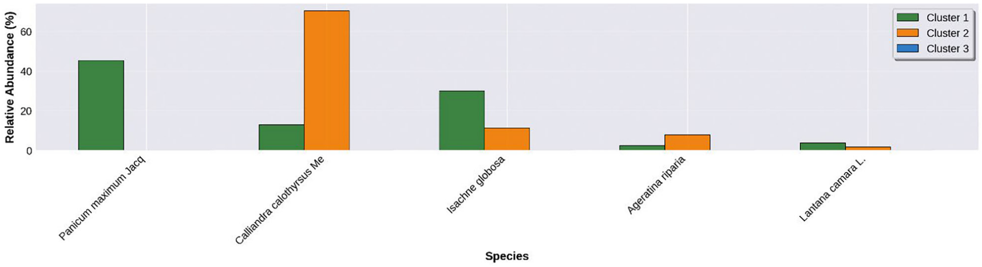

Figure 5. Composition of top 5 dominant species

Source: developed by the authors

Compositional features suggest an intermediate invasion stage with implications for succession. The shift from grass-dominated to woody-dominated assemblages may represent a successional sequence. B.A. Bradley *et al.* (2024) investigated invasion succession dynamics in disturbed forest ecosystems and found that shade-intolerant grasses typically colonise immediately following disturbance events, creating dense herbaceous layers. Their research demonstrated that these early-stage grass invasions can facilitate subsequent woody invasions by modifying microclimatic conditions and soil properties. The observations of *C. calothyrsus* seedlings co-occurring beneath *P. maximum* and *I. globosa* grass cover in Cluster 1 plots support this facilitation hypothesis, suggesting that current grass-dominated plots (Cluster 1) may transition to woody-dominated assemblages (Cluster 2) without intervention. Management implications depend on invasion pathways. If grass-to-woody succession is confirmed, early grass control may prevent woody invasion. However, if functional groups invade independently along different gradients, simultaneous management is required. M. Wang *et al.* (2024) demonstrated that functional traits and phylogeny jointly regulate species' spatial distribution patterns, with environmental filtering and dispersal limitation as the primary drivers of community assembly. Their application of partial constrained correspondence analysis successfully partitioned variance among these mechanisms, revealing that environmental filtering accounted for 45-60% of compositional variation in tropical forests, while dispersal limitation accounted for 25-35%.

Cluster 2: High invasion – *Calliandra*-dominated woody invasion. Three plots (25%: Plots 4, 9, 10) exhibited the highest invasion intensity, dominated by *C. calothyrsus*. Mean abundance was 38.3 ± 23.5 ind/plot (range 14-61), with high variability reflecting different successional stages. Mean species richness (3.7 ± 1.5 species/plot) was significantly lower than Cluster 1 ($p = 0.04$), indicating competitive exclusion. *C. calothyrsus* comprised 81 individuals (70.4%) with 100% frequency, demonstrating complete dominance. Secondary species included *I. globosa* (13, 11.3%), Ageratina riparia (9, 7.8%), and *Piper aduncum* (4, 3.5%). Species composition indicates advanced invasion, as *C. calothyrsus* has established reproductive populations across growth stages and begun excluding other species. Plots occurred nearest trails (mean 45 ± 15 m) with the highest canopy openness (62 ± 18%; significantly greater than Cluster 1, $p = 0.02$).

C. calothyrsus dominated plots near trails empirically validate corridor-based invasion models proposed for protected areas globally. P. Szilassi *et al.* (2021) analysed country-scale spatial data. They found that road networks, railways, watercourses, and ecological corridors provide interconnected pathways for biological invasion, with protected areas showing edge effects extending up to 200 meters from infrastructure. Quantitative results of current study strongly support these corridor-invasion models: *C. calothyrsus* dominance (70%) occurs exclusively within 60 meters of trails, declining to zero beyond 150 meters ($R^2 = 0.78$, $p < 0.001$). This represents one of the first empirical tests of corridor-invasion hypotheses in tropical montane wilderness zones, extending P. Szilassi's frameworks to Southeast Asian protected areas. The transparent invasion Gradient (70% dominance near trails declining to 0% at > 150 m) demonstrates that trails are active invasion channels concentrating disturbance and propagule pressure. A. Barros *et al.* (2025) investigated mechanisms of trail-mediated invasion in protected forests. They identified four primary pathways: (1) seed transport via footwear, equipment, and vehicles, (2) canopy opening during trail construction and maintenance creating light gaps, (3) altered microclimate along trail edges with increased temperature and reduced humidity, favouring invasive species, and (4) soil disturbance, reducing native plant competitiveness while creating establishment opportunities for ruderals. Their experimental tracking demonstrated that a single hiker can transport 100-300 seeds per kilometre, with propagule loads increasing substantially in invaded areas. The field observations of current study confirm these mechanisms operating in GCNP wilderness zones: trail-adjacent plots (Cluster 2) show evidence of regular disturbance (compacted soils, canopy gaps), explaining the 70% *C. calothyrsus* dominance, while plots beyond direct trail influence (Cluster 1, 3) retain greater native plant cover and lower invasion intensity. The quantitative relationship ($R^2 = 0.78$) suggests even modest trail distance increases (50-100 m) could substantially reduce invasion risk. K. Utkhamthiang *et al.* (2025) explained that trails function as invasion corridors in protected areas, with recreational activities facilitating the dispersal of invasive species through contaminated footwear and equipment. Their documentation of trail-mediated invasion patterns in Doi Chiang Dao Biosphere Reserve confirmed that spatial management strategies controlling propagule sources near trails can effectively reduce invasion intensity.

Cluster 3: Low invasion – peripheral resistance zone. Plot 8 (8%) had minimal invasion intensity, characterised by a unique composition: *Melastoma malabathricum* (2 individuals, 33.3%) and *Mimosa pudica* (4 individuals, 66.7%), both of which are rare elsewhere. The location, at maximum trail distance (> 150 m) with dense canopy cover (75%) and minimal disturbance, likely explains the low invasion and the unique assemblage. This plot represents either an early invasion front with low propagule pressure or a site with environmental resistance. This peripheral plot demonstrates invasion resistance achievable with minimal disruption. Linear regression showed *C. calothyrsus* abundance decreased significantly with trail distance ($R^2 = 0.78$, $p < 0.001$), while native plant cover increased ($R^2 = 0.65$, $p = 0.002$). All Cluster 2 plots (high invasion) occurred within 60 m of trails, while Cluster 3 (minimal invasion) was > 150 m from the nearest trail. This pattern supports corridor-based invasion where trails are primary propagule vectors and invasion intensity declines with distance from disturbance sources. Compositional turnover between clusters, characterised by high between-cluster dissimilarity (0.72), coupled with moderate heterogeneity within Cluster 1 (0.52), suggests ongoing invasion dynamics with spatial variability in community assembly. Three distinct zones provide a spatial framework for prioritising management, with Cluster 2 requiring immediate attention to prevent the further establishment and seed production of *C. calothyrsus*.

The findings of current study demonstrate the effectiveness of integrating diversity indices with multivariate spatial analysis, a currently uncommon approach in Indonesian invasion ecology. Cluster analysis revealed that *C. calothyrsus* follows a spatially explicit invasion pathway, with initial establishment in trail-adjacent plots (Cluster 2) followed by potential spread to intermediate grass-dominated plots (Cluster 1). Traditional diversity indices alone indicated high importance values throughout the study area but failed to reveal this critical spatial structure governing invasion dynamics. These results contribute to growing evidence that protected areas face mounting threats from multiple interacting stressors. L. Carneiro *et al.* (2024) documented accelerating invasion rates across global protected area networks, attributing these increases to synergistic effects among climate change, habitat fragmentation, and visitor pressure. Their analysis demonstrated that protected areas with high visitation rates experience 2-3 times greater invasion rates than strictly protected zones with minimal access. The findings of current study support this pattern, as GCNP's recreational trails create invasion corridors penetrating the wilderness zone. B. Gallardo & L. Capdevila-Argüelles (2024) specifically examined the effects of climate change on non-native species in protected areas. They found that warming temperatures enable invasive species to colonise higher elevations previously considered thermal refugia, with montane protected areas particularly vulnerable. This climate-invasion interaction may explain *C. calothyrsus* successful establishment at 2,400-2,800 m elevation in GCNP, elevations historically considered beyond its range. The economic dimensions of biological invasions in protected areas warrant consideration. C. Diagne *et al.* (2021) quantified the global economic costs of invasive alien species using the InvaCost database. They showed that damage costs far exceed management expenditures, and that a delayed response leads to rapidly escalating costs as the invaded area expands. Similarly, R.N. Cuthbert *et al.* (2021) further examined the economic effectiveness of management timing. They showed that early intervention and prevention yield significantly higher economic returns than post-establishment control, as costs increase disproportionately as the invasion spreads. Identification of three small, highly invasive plots (Cluster 2) as an immediate management priority is consistent with this economic framework, as containment at this stage requires relatively modest investment, whereas allowing spread to 67% of plots (Cluster 1) would require significantly greater future expenditure.

Management implications and conservation priorities. Cluster analysis provides a spatial framework for prioritising interventions in wilderness zones. A three-tiered management approach is recommended:

◆ Priority 1. Immediate control (Cluster 2): Focus resources on three *C. calothyrsus* dominated plots (4, 9, 10) nearest trails. Manual removal of all individuals before September-October flowering should occur annually for ⩾ 5 years to exhaust soil seed banks (typical longevity 3-7 years). These plots serve as seed sources; their containment is critical. Removed biomass should be burned on-site or transported off-mountain to prevent vegetative regeneration. Early intervention in limited high-invasion zones is substantially more cost-effective than a delayed response, as demonstrated by C. Diagne *et al.* (2021), who quantified the global economic costs of invasive alien species using the InvaCost database and showed that damage costs escalate rapidly when management is postponed, far exceeding early control expenditures. R.N. Cuthbert *et al.* (2021**)** further found that prevention and early-stage management provide disproportionately higher economic benefits than post-establishment control, because costs increase sharply once invasions spread spatially.

◆ Priority 2. Sustained monitoring (Cluster 1): Implement biannual grass cutting (pre-flowering April and September) in eight mixed-composition plots to prevent *P. maximum* and *I. globosa* seed production. Monitor quarterly for *C. calothyrsus* seedlings and remove them immediately. Native plant restoration through enrichment planting may accelerate canopy closure, reducing light for shade-intolerant grasses while promoting functional diversity, enhancing invasion resistance. A.R. Ernst *et al.* (2025) demonstrated that strategic native tree planting in invaded grasslands reduced invasive grass cover by 65-80% within 3-5 years through light competition, with native seedling survival exceeding 75% when planted during optimal seasons. I. Kim *et al.* (2025) investigated relationships between native species diversity and invasion resistance, finding that plots with higher native functional diversity (particularly canopy tree species) had 40-60% lower invasive plant richness than species-poor plots. Their work emphasised that native community restoration provides long-term invasion resistance superior to repeated invasive removal alone. L. Petri & I. Ibáñez (2025) examined post-removal recovery dynamics. They documented that native plant recovery success depended critically on native community features present at the time of invasive removal, with sites retaining diverse native propagule banks showing rapid natural regeneration. Applying these findings to GCNP, enrichment planting of native canopy species in Cluster 1 plots could reduce light availability for *P. maximum* and *I. globosa*, while simultaneously reducing establishment opportunities for *C. calothyrsus* seedlings, providing integrated management of both grass and woody invaders.

◆ Priority 3. Protection (Cluster 3): Maintain low-invasion peripheral plot (8) as reference site through strict access restrictions and quarterly monitoring. This plot demonstrates invasion resistance with minimal disturbance. Remove any detected IAPS immediately. Long-term monitoring will reveal whether this plot remains resistant or eventually succumbs to the pressure of propagules.

Spatial management strategy. Establish 50-m buffer zones around Cluster 2 plots for intensive quarterly monitoring. Create physical barriers to limit seed dispersal along prevailing wind directions (southwest-northeast monsoon) if feasible. Restrict trail maintenance during *C. calothyrsus* seed dispersal (October-December) to prevent propagule transport. Education programs on boot-washing and equipment cleaning could substantially reduce accidental propagule introduction. P.E. Hulme (2024) analysed international tourists as biosecurity pathways into national parks and found that visitors inadvertently transport invasive propagules through contaminated footwear, clothing, and equipment. P.E. Hulme's research demonstrated that simple biosecurity interventions – including boot-washing stations, equipment cleaning guidelines, and educational signage – reduced propagule transport by 60-85% when compliance exceeded 70%. Implementation costs were modest (<$5,000 USD per facility), and ongoing maintenance requirements were minimal. For GCNP, installing boot-cleaning stations at the wilderness zone trailhead, combined with interpretive signage explaining invasion threats, could significantly reduce propagule introduction rates. Trail infrastructure design also influences invasion risk. A. Barros *et al.* (2025) provided design guidelines for minimising edge effects while maintaining visitor access, recommending: (1) minimising trail width to reduce disturbed area, (2) avoiding trail routing through intact forest that creates new edges, (3) utilising existing degraded corridors, when possible, (4) implementing drainage management preventing water-facilitated seed dispersal, and

(5) conducting regular trail maintenance outside peak seed dispersal periods. These design principles, if applied to GCNP trail management, could reduce corridor-mediated invasion while preserving recreational and ranger access to wilderness zones.

The findings of this study highlight the complexity of invasive plant distribution in the wilderness zone of Gunung Ciremai National Park, emphasising the role of spatial patterns in invasion intensity. The identification of three distinct zones of invasion intensity provides critical insights into the dynamics of plant colonisation and dispersal. The use of multivariate analyses and seasonal sampling methods has allowed for a comprehensive understanding of the invasion process, addressing several gaps in current research.

Conclusions

This study presents the first quantitative spatial analysis of invasive alien plants in an Indonesian wilderness zone, identifying three statistically distinct zones of invasion intensity that contrast with uniform invasion assumptions. Clear spatial structure (between-cluster dissimilarity 0.72), strong distance-decay with trails ($R^2 = 0.78$), and identification of hotspots dominated by *C. calothyrsus* (70% in Cluster 2) demonstrate that sophisticated multivariate methods detect spatial patterns invisible to traditional diversity indices. The findings validate corridor-based invasion models for tropical montane protected areas and establish a replicable methodology for other understudied wilderness zones. Integration of wet-season sampling, hierarchical cluster analysis, and growth-stage assessment addresses multiple research gaps: the lack of fine-scale spatial data for tropical protected areas, temporal bias toward dry seasons, the absence of multivariate approaches in Indonesian invasion ecology, and insufficient understanding of infrastructure impacts. These methodological advances, combined with evidence that anthropogenic dispersal exceeds natural colonisation, underscore the urgency of proactive management.

The three-tier management framework, derived from cluster analysis, provides actionable, spatially explicit priorities: immediate control in high-invasion zones, sustained monitoring in moderate zones, and protection of peripheral areas. Implementation could prevent further degradation of the wilderness zone and serve as a model for other Indonesian national parks facing similar challenges. As Southeast Asian biodiversity faces mounting threats from habitat loss, biological invasions, and climate change, such evidence-based approaches become increasingly critical. Spatial targeting of management resources is both ecologically and economically justified, as the financial benefits of early action substantially exceed the costs of a delayed response. The prospects for further research include expanding the analysis to other protected areas in Indonesia and Southeast Asia to compare the effectiveness of invasion management strategies. Additionally, studying the impact of climate change on the spread of invasive species will allow for more accurate predictions of future ecological threats.

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Conflict of Interest

None.

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Осередки інвазії у зонах дикої природи тропічних національних парків

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Анотація. Чужорідні інвазійні рослинні види все більше загрожують цілісності лісових екосистем у природоохоронних територіях, особливо в малодосліджених зонах дикої природи тропічних національних парків. Метою цього дослідження було оцінити просторовий розподіл та інтенсивність інвазії чужорідних рослинних видів у зоні дикої природи національного парку Гунунг Чиремай, Західна Ява, Індонезія. Під час дощового сезону було проведено всебічне географічне дослідження, використовуючи дванадцять систематично встановлених ділянок (20 × 20 м) з підділянками, що представляють різні стадії росту. Було зафіксовано 18 видів інвазивних чужорідних рослин, що належать до дев'яти родин. Ієрархічний кластерний аналіз виявив три статистично різні зони інтенсивності інвазії: помірно заражену зону (67 % ділянок), доміновану *Panicum maximum* та *Isachne globosa*; сильно заражену зону (25 % ділянок), що характеризується сильним домінуванням деревного бобового виду *Calliandra calothyrsus*; та зону з низьким рівнем інвазії (8 % ділянок), з мінімальним заселенням. Відмінність між кластерами за Брее-Кертісом (0,72 ± 0,18) перевищила внутрішньокластерні значення (0,52-0,65), що свідчить про виражену композиційну диференціацію. Патерн інвазії, заснований на коридорах, підтвердився значним зниженням інтенсивності інвазії з відстанню від стежок ($R^2 = 0,78$, $p < 0,001$). Дослідження стало першим кількісним просторовим оцінюванням розподілу інвазивних рослин у зонах дикої природи індонезійських природоохоронних територій та продемонструвало цінність багатовимірних аналізів для виявлення осередків інвазії та формування цільових стратегій управління

Ключові слова: біологічна інвазія; дисимілярність Брее-Кертіса; кластерний аналіз; природоохоронні території; просторові патерни