



Plant Diversity and Community Structure in the Highland Savanna of Bromo Tengger Semeru National Park

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ABSTRACT

Disturbances continually decline savanna plant diversity, yet Indonesian research historically favors forests and lowland tropical savannas (e.g., Baluran and East Nusa Tenggara), leaving montane savannas understudied. Given these dynamic shifts, establishing baseline plant diversity data is imperative. This study specifically aims to evaluate plant diversity, community structure, and their relationship with abiotic parameters in Bromo Tengger Semeru National Park's disturbed montane-subalpine savanna. Vegetation sampling used 30 plots (10 m x 5 m based on minimum curve area), measuring plant density, cover, abiotic factors, and soil microorganisms (three replications). Diversity was evaluated using the Shannon-Wiener index (H'), and dominance using the Importance Value Index (IVI) and cover percentage. Spearman's correlation was used to examine the relationship between species richness and environmental factors. Vegetation inventory identified fifteen plant species belonging to nine families, with a diversity index (H') of 1.81. *Pteridium aquilinum* heavily dominated the community structure (IVI = 69.44%), followed by *Imperata cylindrica* (55.08%). The low-to-moderate plant diversity observed in the Bromo savanna is likely driven by the peak dry season and the heavy dominance of invasive species. These data contribute to the ecological baseline database of the national park, providing a crucial reference for future monitoring of vegetation dynamics.

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INTRODUCTION

Savannas are dynamic and highly adaptive ecosystems characterized by expanses of grassland, interspersed with scattered trees or shrubs (Buisson et al., 2019; Perdinan et al., 2024). These savannas contribute to the global carbon cycle, accounting for approximately 30% of all terrestrial primary vegetation production and providing a range of essential ecosystem services for living organisms (Russell-Smith & Sangha, 2018), one of which is plant diversity (Wilsey, 2018). Savannas are home to an extraordinary and unique biodiversity, structurally adapted to a climate characterized by distinct wet and dry seasons and frequent fires (Solbrig et al., 1996; Laurila-Pant et al., 2015; Penington et al., 2018). Within these environments, floristic diversity is not uniformly distributed but is instead governed by complex spatial arrangements and life-form stratifications. Consequently, characterizing

the structural partitioning of these botanical components is vital, particularly in unique high-altitude savannas where extreme environmental filtering directly reshapes plant diversity and community assembly (Sarmiento, 1984).

Plant diversity in savannas is crucial due to the coexistence of herbs, C₄ grasses, shrubs, and trees. Savanna diversity varies uniquely according to its vegetation layers. Tree diversity is low due to intense sunlight, minimal rainfall during the dry season, and seasonal fires, which means that only a few tree species survive (Sutomo, 2016). These trees grow sparsely and do not form a dense canopy. However, the lower layers, consisting of grasses and shrubs, exhibit high diversity. Because the tree canopy is not dense, sunlight penetrates to the ground. This allows for the emergence of various species of grasses, herbs, shrubs, and even seasonal flowering plants (Solbrig et al., 1996). This mosaic vegetation structure uniquely divides ecological roles between the lower layers (grasslands) and the upper layers (tree canopies) (Perdinan et al., 2024). Different grass species have different growth cycles, ensuring an uninterrupted food supply for herbivorous mammals, both during the rainy season and extreme dry seasons (Pennington et al., 2018).

Unfortunately, savanna ecosystems face disruptions from both natural and human-made factors. The impacts of human activities are causing widespread and accelerating savanna degradation. Key threats include land cover change and transformation, landscape fragmentation that disrupts herbivore communities and fire regimes, climate change, the presence of invasive species, and increased atmospheric CO₂ (Osborne et al., 2018; Williamson et al., 2024). The level of degradation of tropical savanna ecosystems globally is currently critical, with less than 3% of the world's tropical savanna remaining intact and over sixty percent of protected savanna ecosystems exhibit degraded ecological conditions, leading to an ongoing erosion of their biodiversity integrity (Williams et al., 2022; Gebremedhn et al., 2023). In Indonesia, the extent of savanna degradation nationally is not recorded in a single official figure because the government generally groups these areas into categories of critical land or forest and land fires. However, the overall picture of the damage is generally reported specifically through two main savanna areas in Indonesia, namely East Nusa Tenggara and Baluran National Park (Sabarno, 2002; Sutomo et al., 2016; Kurniawan & Yuniati, 2015).

The Bromo Tengger Semeru National Park (BTSNP) savanna is one of the savannas in Indonesia. Located at an altitude of around 2,300 meters above sea level (masl), this savanna presents a unique view in the form of a combination of harsh volcanic landscape with hilly green vegetation (Firmansyah, 2018). In contrast to the lowland savanna which is dry and arid like in Nusa Tenggara, the Bromo Savana is a montana savanna with relatively high air humidity (42%–45% to 90%–97%) with an annual precipitation ranging from 1,600 to 1,800 mm, the ecosystem receives adequate moisture to sustain green vegetation throughout most of the year, except during the height of the arid period. This moisture regime is coupled with a cold thermal climate fluctuating between 3°C and 18°C, which occasionally drops below freezing point (BMKG, 2024a). The beautiful landscape and cool temperatures make it one of the national parks with the highest level of tourist visits in Indonesia (KLHK, 2020). However, this has caused environmental degradation (Azhari et al., 2025). In addition, since 2014 the savanna has experienced several fires with an affected area of up to 1,500 ha.

The high diversity and potential of savanna plants in BTSNP, which is accompanied by the potential threat of reduced diversity and even the loss of plant species, is the reason why it is necessary to conduct an analysis of plant diversity. To date, the most recent comprehensive baseline assessment of vegetation across the wider Bromo Tengger Semeru National Park (BTSNP) ecosystem remains the work by Qurrota (2010). A rigorous evaluation of peer-reviewed databases, institutional repositories of regional universities, and park management reports from 2010 to 2024 confirms a significant data gap. While specialized studies have emerged during this 14-year period, they are strictly constrained to specific ecologies or events, such as post-fire succession and diversity within burned patches (Novitasari, 2018; Azka, 2025; Ramadhani, 2026), alpine vegetation within the Bromo crater vicinity or agroforestry configurations in the park's buffer zones (Zayadi et al., 2024). Consequently, a comprehensive, broad-scale ecological study of the park's overall vegetation structures has been completely absent for nearly a decade and a half. This prolonged data gap severely limits the baseline information required for effective macro-level conservation policies. This study directly addresses this critical deficiency by providing the first integrated and comprehensive

vegetation analysis of BTSNP since 2010. Without regularly and consistently updated data, drastic changes such as savannah destruction or the extinction of endemic plants will not be detected early (Tudorescu et al., 2024). Furthermore, this is crucial considering that BTSNP is one of 56 national parks in Indonesia and is listed by UNESCO as a World Biosphere Reserve Network due to its unique ecosystems, including deserts, sand seas, and savannas (Wibowo et al., 2021).

MATERIALS AND METHODS

Study Area and Materials

The research took place in the savanna of Bromo Tengger Semeru National Park (BTS NP), East Java, Indonesia, at $7^{\circ} 59' 02.94''$ S and $112^{\circ} 56' 46.89''$ E (Figure 1). The Bromo savanna is classified as a Subtropical Highland Climate (Cwb, Köppen-Geiger climate; Rudolf, 1954). This research conducted in August 2024, during the dry season. The study took place in a savanna area-a site intensively impacted by vehicular traffic, including cars and motorcycles, alongside tourism-related disturbances.

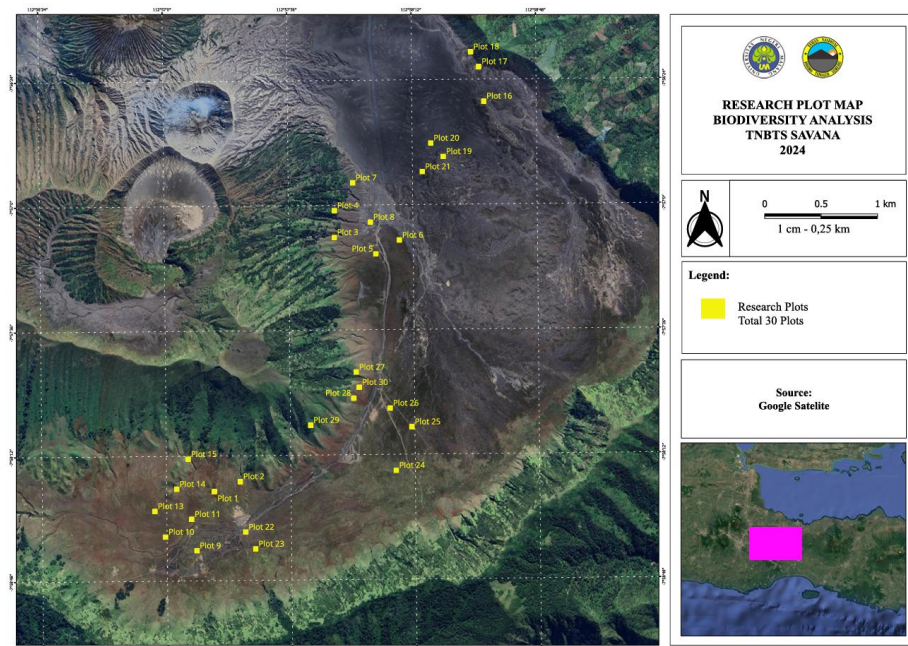


Figure 1. The research area in savanna of Bromo Tengger Semeru National Park, Indonesia

Field Survey Methods

Sampling points were randomly selected according to a preliminary study. At each sampling point, vegetation was recorded using the plot method with a quadrat size of $10\text{ m} \times 5\text{ m}$, which was established as the minimum area. This specific sampling size was determined based on the standard ecological threshold where a progressive increase in plot area no longer yields an increase in the number of recorded species by more than 10% (Oosting, 1958). To ensure representativeness, this dimension was derived from the maximum plot size stabilized across ten independent minimal area curves (Supplementary Table 1). A total of 30 sampling points were established (Figure 1); every species of plant in the plot was documented, along with the plant cover. Plant species were identified using Flora of Java by Backer et al. (1965) and Flora Malesiana (Vol. 6, Issue 3, p. 431) by van steenis & van Steenis-Kruseman (1950). Plant nomenclature and the geographic origin of the studied taxa were determined according to Plants of the World Online (POWO, 2026). The coordinates of each sampling point were obtained by GPS (Garmin GPS 60, USA).

Measurements of Microclimate

Light intensity (Lux, Extech 407026 Light Meter with PC Interface, USA), relative humidity (%), air temperature ($^{\circ}\text{C}$, Elcometer 116C Sling Thermohygrometer, UK), soil temperature ($^{\circ}\text{C}$, Digital

Soil Thermometer, USA), pH value and moisture (%) were measured using the soil tester (Takemura DM-5, Japan) at three randomly selected points in each plot. Using a 5 cm diameter corer, samples of substrates were taken from three randomly selected locations at each site along the range of rooting depth (0–30 cm) for microorganism analysis. Agar plate counts were used to determine the number of bacteria and fungal colonies on the substrate (CFU, Colony Forming Unit).

Data Analysis

A variety of vegetative indicators were derived for all species at every plot, including (a) cover, (b) relative cover, (c) density, (d) relative density, (e) frequency of occurrence, (f) relative frequency, and (g) important value index. Furthermore, the overall amount of covered vegetation was calculated. In this study, The Shannon diversity index (H') of the BTS NP savanna was used to determine the plant diversity in savanna. This index was calculated using the following equation (1) (Magurran, 2004). Abiotic factor data were analyzed descriptively. The relationship between abiotic factors and the number of species was analyzed using Spearman's correlation at a significance level of 5% using SPSS 26.0.

$$H' = -\sum_{i=1}^S (P_i \ln P_i) \quad (1)$$

H' = Shannon-Wiener diversity index

s = Species richness (the total number of species recorded)

P_i = The proportion of individuals belonging to the i -th species relative to the total number of individuals in the sample ($P_i = n_i/N$), where n_i represents the individual abundance of species i , and N is the total number of individuals across all species

$\ln$ = The natural logarithm

RESULTS AND DISCUSSION

Floristic Diversity and Distribution

A total of 15 plant species from 9 families were found across 30 random sampling points. Seven of these species are native to Indonesia: *Marsilea crenata*, *Parochetus communis*, *Imperata cylindrica*, *Leptochloa chinensis*, *Ischaemum rugosum*, *Themeda gigantea*, and *Vaccinium varingiiifolium*. Additionally, *Styphelia javanica* is endemic to East Java, while the remaining species are introduced. Two species are shrubs, and the other 13 species are herbs (Table 1). Savannas are generally characterized by the dominance of C4 grasses, species, which have additional steps in the photosynthetic process, making photosynthetic pathways that capture CO₂ more suitable for warmer conditions (Krebs, 2014; Griffith et al., 2015; Hutley & Setterfield, 2018); however, our findings indicate a deviation in the Bromo savanna. Although the Poaceae family possessed the greatest number of species, the highest coverage was recorded by *Pteridium aquilinum* (Dennstaedtiaceae).

Pteridium aquilinum (IVI = 69.44) is the dominant species, followed by *Imperata cylindrica* and *Nassella trichotoma*, with IVI are 55.08 and 40.77, respectively. More than 70% of the savanna is covered by *Pteridium aquilinum* (40.22%) and *Imperata cylindrica* (33.16%) (Figure 2). Both species were found in 28 plots and in 21 plots out of 30 sampling plots. Meanwhile, the native species, *Marsilea crenata*, was only found in one plot (the 28th plot) with 1 individual; *Vaccinium varingiiifolium* was found in 1 plot (plot 17) with 1 individual. The endemic species, *Styphelia javanica*, was found in 2 plots (plots 5 and 19) with 48 and 3 individuals, respectively.

The dominance of *Pteridium aquilinum* in savanna ecosystems is partly driven by excessive fire frequencies (Mkungu et al., 2023). When fire destroys above-ground vegetation, the species' robust underground rhizomes enable rapid resprouting, allowing it to outcompete and preempt native grasses. The Bromo savanna is highly prone to wildfires, driven by both prolonged dry seasons and anthropogenic activities. Notably, significant fire events were documented in 2014, 2015, 2018, and 2023 (Suprihantini et al., 2016; Suhardono et al., 2024; Nugraha, 2025). Moreover, *Pteridium aquilinum*

is regarded as being among the most adept worldwide invasive plant species. Its distribution is tied to human-caused changes in land usage processes, such as agricultural and livestock operations. This species thrives when light is abundant (Amouzgar et al., 2021). *P. aquilinum*'s allelopathic properties,

Table 1. Plants species at Savanna of Bromo Tengger Semeru National Park

No.	Plant Species	Life form	Family	Original	H'	IVI	RC	RD	RF
1	<i>Andropogon gerardi</i> Vitman	Ph	Poaceae	Central and North America	0.18	13.6	2.44	6.39	4.76
2	<i>Equisetum hyemale</i> Lour	Pf	Equisetaceae	Temperate regions of Eurasia and North America	0.02	8.49	3.27	0.46	4.76
3	<i>Parochetus communis</i> Buch. - Ham. Ex D. Don	Ah	Fabaceae	Indian Subcontinent to China (Sichuan, Yunnan) and Indo-China, S. Malesia	0.36	34.2	0.79	31.51	1.9
4	<i>Foeniculum vulgare</i> Miller	Ph	Apiaceae	Mediterranean to Ethiopia and West Nepal	0.14	9.14	0.59	4.75	3.81
5	<i>Imperata cylindrica</i> (L.) Raeusch.	Ph	Poaceae	Southeast Asia and East Africa	0.08	55.08	33.16	1.92	20
6	<i>Leptochloa chinensis</i> (L.) Nees	Ph	Poaceae	Australia, China, South Asia, southern and eastern Africa, and throughout the Pacific basin	0.04	23.89	14.5	0.82	8.57
7	<i>Marsilea crenata</i> Presl.	Pf	Marsileaceae	Southeast Asia	0.01	1.22	0.17	0.09	0.95
8	<i>Nassella trichotoma</i> (Nees) Hack. & Arechav.	Ph	Poaceae	South Brazil to Argentina	0.37	40.77	1.07	35.89	3.81
9	<i>Plantago major</i> L.	Ph	Plantaginaceae	Europe, northern and central Asia	0.1	6.72	0.17	2.74	3.81
10	<i>Ischaemum rugosum</i> Salisb.	Ph	Poaceae	Tropical Africa, Tropical & Subtropical Asia to W. Pacific.	0.02	3.37	0.24	0.27	2.86
11	<i>Pteridium aquilinum</i> (L.) Kuhn	Pf	Dennstaedtiaceae	Eurasia and North America	0.09	69.44	40.22	2.56	26.67
12	<i>Styphelia javanica</i> (Zoll. & Moritz) J.J.Sm.	Ps	Ericaceae	East Java	0.14	7.15	0.59	4.66	1.9
13	<i>Themeda gigantea</i> (Cav.) Hack. ex Duthie	Ph	Poaceae	Bismarck Archipelago, Maluku, New Caledonia, New Guinea, Philippines, Solomon Is., Vanuatu	0.12	13.07	1.03	3.47	8.57
14	<i>Vaccinium varingiaefolium</i> (Blume) Miq.	Ps	Ericaceae	Java, Lesser Sunda Is., Malaya, Sumatera	0.01	1.39	0.34	0.09	0.95
15	<i>Verbena brasiliensis</i> Vell.	Ah	Verbenaceae	Brazil	0.14	12.46	1.41	4.38	6.67
Total					1.81	300	100	100	100

Note: Ah = Annual herb; Pf = Perennial fern; Ph = Perennial herbs; Ps = Perennial shrubs

H' = Shannon-Wiener diversity index; IVI = Important Value Index; RC = Relative Cover; RD = Relative Density; RF = Relative Frequency



Figure 2. Vegetation cover within the Bromo savanna ecosystem during the peak dry season (August 2024), where the landscape is predominantly covered by *Pteridium aquilinum* (40.22%) and *Imperata cylindrica* (33.16%).

The red arrows highlight the representative patches of *P. aquilinum* displaying a distinctive dried greyish coloration, while the blue arrows point to *I. cylindrica*, characterized by its yellowish-brown (tan) appearance

as well as its capacity to tolerate a variety of soil and environmental circumstances, have contributed to the colonization of almost all terrestrial habitats, with the exception of deserts (Mira et al., 2021). It has a strong potential for colonization due to its underground rhizome, which may grow up to 2 m in one growing period, giving them a high colonization potential. Furthermore, the dense canopy creates a physical barrier that prevents the establishment of indigenous species (Baptiste, 2019).

Imperata cylindrica is also known to be part of the world's top ten worst weeds and among the top 100 most invasive plants. It is an adept colonizer, forming vast monospecific stands across numerous nations. Through leachates, root exudation, or plant part decomposition, *I. cylindrica* releases its allelochemicals into the rhizosphere soil and nearby environments. Some allelochemicals have the potential to alter the community of microorganisms, such as rhizobia and mycorrhizal fungi, which would hinder the seed germination and growth process of indigenous species of plant regeneration. As a result, *I. cylindrica*'s allelopathy may promote invasiveness, naturalization, and the establishment of huge monospecific stands (Kato-Noguchi, 2022). *I. cylindrica* competes for nutrients more effectively than native pine savanna plants, absorbing more nitrogen, phosphate, and potassium (Tierny & Wurzbürger, 2024). It has been demonstrated that the species limits the amount of nitrogen and water available in the nearby soil, which reduces the capacity of young *P. taeda* to grow by 50% (Danesghar & Jose, 2009). Based on the results obtained, we presume that the presence of invasive species in this savanna can be one of the major factors that cause the loss of endemic species in the future. Further research and efforts to control invasive plants are needed in the savanna.

Although *Nassella trichotoma* is not classified among the most hazardous global weeds, its presence poses a critical threat to native floral species. This grass is highly eurythermal, possessing a broad thermal tolerance that enables it to withstand extreme cold conditions and soil freezing in mountainous regions. Furthermore, *N. trichotoma* exhibits a high tolerance to drought, which is attributed to its fine and fibrous root system situated predominantly within the top 20–30 cm of the soil profile (Humphries & Florentine, 2021). These physiological and edaphic adaptations explain its pronounced dominance within the Bromo savanna ecosystem. Additionally, its leaves are highly sclerophyllous; this adaptive trait allows the plant to effectively resist prolonged drought, intense grazing, and depleted soil nutrient levels, particularly in environments characterized by severe phosphorus deficiencies (Distel et al., 2007).

The pronounced dominance of three specific plant taxa directly accounts for the suppressed floral diversity observed within the ecosystem, where the Shannon–Wiener diversity index (H') was recorded at 1.80 (Table 1). According to the empirical framework established by Magurran (2004),

which posits that typical biological communities exhibit (H') values ranging between 1.5 and 3.5, the Bromo savanna falls squarely into a low-to-moderate diversity classification. This positioning signals a highly skewed distribution of species abundance, driven by the monopolization of available niches by these dominant species. Functionally, this low-to-moderate diversity classification implies a compromised ecological resilience within the BTSNP savanna. Such diminished biodiversity severely impairs the ecosystem's buffering capacity, rendering it highly vulnerable to environmental perturbations such as pest outbreaks and climate-driven stresses. Furthermore, this polarized structure accelerates the competitive exclusion and subsequent displacement of critical native endemics, most notably *Styphelia javanica*, thereby driving a trajectory toward local biotic homogenization and a permanent decline in the park's biodiversity integrity.

Although these results provide critical insights, they reflect specific seasonal and spatial parameters that define the scope of this research. First, data collection was conducted exclusively during the peak dry season in August 2024. Consequently, the recorded plant diversity index ($H' = 1.81$) likely represents a substantial underestimate of the actual annual community composition. Many typical savanna plant species exhibit ephemeral, geophytic, or dormant life strategies during extended dry periods, rendering them undetected during our sampling period (Abreu et al., 2017). However, capturing this low diversity state during the environmental climax of the dry season remains a valuable core finding of this research.

Additionally, a spatial sampling bias emerged due to constraints regarding logistical accessibility and field safety. Sampling quadrats were predominantly located within accessible zones characterized by high-intensity tourism and frequent vehicle transit toward the Mount Bromo volcanic complex. The continuous anthropogenic pressure inherent to these locations may artificially depress species richness and distort vegetation community structures compared to pristine habitats. Hence, caution is advised when extrapolating these metrics to represent the wider Bromo savanna ecosystem. To delineate a comprehensive ecological baseline, subsequent investigations should implement multi-seasonal tracking particularly during the peak wet season and extend sampling efforts into non-disrupted interior sectors.

The number of plant species identified during this study is lower than that reported in 2010, which documented 28 species consisting of 14 shrubs and 14 herbs (Qurrota, 2010). This decrease in the number of species and the lower plant diversity might be driven by several ecological drivers. First, the presence of introduced invasive species has enabled certain dominant taxa to exert control over the savanna area. Species' functional characteristics strongly influence ecosystem properties and community assembly (Hooper et al., 2005; Mbangilwa et al., 2019). Second, the decline is closely linked to the global climate anomaly in the Pacific Ocean, which triggered an above-normal dry season across several regions in Indonesia, including East Java. This anomaly culminated in a peak dry season in August 2024 (BMKG, 2024b), precisely when our measurements were taken. Under such prolonged water deficit, only drought-tolerant plant species can survive. The impacts of climate change in recent years have become increasingly visible, with widespread vegetation mortality reported across various ecosystems, including savannas (Sankaran, 2019). Therefore, continued seasonal monitoring is highly recommended to comprehensively map the actual plant diversity and its long-term dynamics in the savanna.

However, the apparent decline in species richness and diversity index compared to the 2010 data must be carefully interpreted through the lens of methodological and seasonal discrepancies. The previous study employed smaller but more numerous sampling units (25 plots of 1 m × 1 m for herbs and 2 m × 2 m for shrubs) during February 2010, which corresponds to the peak wet season. In contrast, our study utilized larger but fewer plots (30 plots of 10 m × 5 m) during the peak dry season (August 2024). These variations heavily act as confounding factors; the wet season sampling inherently captures a high abundance of ephemeral and annual herbs that emerge only under high water availability, inflating the diversity indices. Conversely, peak dry season conditions induce severe desiccation and dormancy in these lower-stratum species, leading to an underrepresentation of active flora (Hassler et al., 2010; Shimadzu et al., 2013). Therefore, the lower diversity value observed in this study likely reflects a combination of seasonal phenological shifts and sampling design variations, rather than a definitive long-term biodiversity loss.

Presence and Distribution of Endemic Plant Species

Amidst the high dominance of *Pteridium aquilinum* and *Imperata cylindrica*, *Styphelia javanica* an endemic shrub restricted to the tropical mountain biome of East Java is still present. However, its spatial occupancy is highly restricted, occurring in only 6.67% of the sampling locations. Specifically, the species was recorded in merely two out of 30 plots with a minor total coverage of 0.59%. This highly skewed distribution, characterized by a stark contrast in density (48 individuals in plot 5 vs. 3 individuals in plot 19), strongly indicates an aggregated or clumped dispersion pattern. Such a narrow and localized distribution underscores the species' highly specialized environmental tolerances (Cho et al., 2024), which inherently increases its vulnerability to localized extinction (Krebs, 2014; POWO, 2025).

Field observations reveal that this clumped pattern is tightly linked to the species' ecophysiological traits; *S. javanica* is a shade-intolerant, heliophilic shrub that strictly requires open areas with direct solar radiation for optimal growth. However, our vegetation cover data demonstrate that more than 70% of the Bromo savanna landscape is aggressively dominated by *P. aquilinum* and *I. cylindrica*. The broad, dense fronds of *P. aquilinum*, in particular, create substantial canopy shading that heavily limits light penetration to the lower stratum (Maulidah, 2026). This extensive structural dominance imposes a severe competitive exclusion effect, drastically restricting the microhabitat availability for *S. javanica*. Consequently, plots 5 and 19 likely represent rare, localized open refugia or historical disturbance footprints that remain unencroached by these dominant weeds, allowing *S. javanica* to establish clustered populations.

Paradoxically, as an endemic taxon, *S. javanica* is evolutionarily well-adapted to the unique ecological conditions of its native habitat (Coelho et al., 2020). Nevertheless, its restricted and fragmented occupancy suggests that its evolutionary resilience is currently being challenged by severe habitat squeezing and demographic stochasticity. Any further expansion of dominant weeds could eliminate these critical microhabitat gaps, threatening the localized persistence of this endemic species. Therefore, further research is urgently required to evaluate its long-term adaptability to exotic plant encroachment and the compounding effects of global climate change to ensure its sustainability in the savanna.

Styphelia javanica is an endemic plant of East Java (Govaerts et al., 2021; Kartawinata & Sudarmonowati, 2022; POWO, 2025). The local community, Tengger tribe, calls it “Suket Melelo or Ladingan”, a typical plant found in several savanna blocks of BTSNP. This species is a small shrub (Figure 3) that grows in marginal places as a pioneer plant. In Java, it is only found on Mount Arjuno, Mt. Penanggungan, Mt. Kawi, Mt. Tengger Semeru, and Mt. Iyang. Included in the Ericaceae family, this species has a limited and specific distribution area. Most are only found in highland and hilly areas with rocky, hard soil conditions (van Steenis, 2006). Plants of the world online (POWO) includes this species as one of the Angiosperma species predicted to be at risk of extinction (POWO, 2025). In 2022, BTSNP management carried out monitoring of *Styphelia javanica* as part of an effort to conserve this species (Maya, 2022).

Microclimatic and Microbial Properties

Data collection was conducted in the peak of the dry season, which caused almost all plants in the savanna to experience drought (Figure 4). Aboveground, plant organs are generally brown, while *Pteridium aquilinum* is silver gray. These dry leaves and stems are fire materials that cause savanna to be easily flammable (Ortiz et al., 2023). This condition is also reflected in environmental data; the results of microclimate measurement describe the dry conditions of the savanna, i.e., high air temperature (31°C), air humidity (64.4%), and the soil temperature (30°C). However, soil humidity is still classified as humid (52.2%) (Table 2).

The presence and development of vegetation in the tropics may be attributed to the high soil moisture content (Novianti et al., 2018), including in the savanna during the dry season. Temperature contributes more than 90% to both phylogenetic and functional plant diversity, which showed that climate plays a greater role (Wang et al., 2024). The light intensity is classified as high with a high standard deviation due to the difference in intensity in the morning, afternoon, and evening. High light

intensity and temperature conditions, along with limited water availability, are conditions to which C4 plants are adapted (Bouchenak-Khelladi et al., 2020). This is one of the explanations for why C4 species dominate the savanna. The herbaceous component of the savanna serves as the system's governing factor, regulating essential ecological processes such as productivity, water balance, fires, mineral cycling, and herbivory. The common species have broad regional distributions, yet each has its distinct phenology and microdistribution. Although the herbaceous stratum is regarded as continuous, it is only so at the peak of its growth, considering the actual basal area of the grasses can be just 10-20% (Perdinan et al., 2024).



Figure 3. Life-form of *Styphelia javanica* collected from savanna ecosystem of Bromo Tengger Semeru National Park, Indonesia, in August 2024 demonstrating a relatively short shrub growth form. The included ruler serves as a visual scale (red line), highlighting that the specimen reaches a height of approximately 11 cm

In this study, the measured soil bacterial and fungal numbers across the savanna plots were relatively low, yielding 68×10^3 CFU/g and 60×10^3 CFU/g, respectively. These low microbial counts, coupled with the strongly acidic soil condition (pH = 5.1), imply a compromised state of soil health and suppressed biological activity within the Bromo Tengger Semeru National Park (BTSNP) ecosystem. This biological suppression is likely exacerbated by excessive soil acidity, nutrient leaching, and the environmental stresses inherent to high-altitude savannas (Pellegrini, 2016; Novianti et al., 2021).



Figure 4. Impact of seasonal drought on the savanna vegetation of the Bromo Tengger savanna ecosystem observed in August 2024. The aboveground biomass exhibits a widespread shift to silvery-grey and faded brown colorations, serving as a generalized visual indicator of drought-induced vegetation degradation across the entire study area

Table 2. Environmental Factors in Savanna

Abiotic factor	Value
Air temperature (°C)	31.4 ± 3.4
Air humidity (%)	64.4 ± 7.2
Soil temperature (°C)	30.0 ± 3.0
Soil moisture (%)	52.2 ± 4.2
Soil pH	5.1 ± 0.9
Light intensity (K.lux)	222.1 ± 86.6
Soil microorganism (m.o)	Number
Bacteria (CFU)	68 x 10 ³ ± 51 x 10 ³
Fungi (CFU)	60 x 10 ³ ± 28 x 10 ³

Note: mean ± standard deviation; n = 100 (abiotic factors); n = 9 (soil m.o)

Furthermore, the distinct altitudinal gradient and extreme climatic factors characteristic of highland savannas create a highly challenging microenvironment that naturally constrains microbial proliferation (Hutley & Setterfield, 2008; Srikanthasamy et al., 2018). In contrast, healthy soils typically harbor between 10⁶ and 10⁸ culturable bacteria per gram of soil; values falling below the 10⁶ threshold signify poor soil health, which is frequently driven by nutrient deficiencies and altered soil chemical properties (Ratnakar & Shikha, 2018).

The Correlation Between Species Richness and Environmental Factors

Based on the Spearman correlation analysis, no individual abiotic factor exerts a statistically significant influence on plant species richness within the Bromo Tengger Semeru National Park (BTSNP) savanna ($p > 0.05$; Table 3). Ecologically, this lack of significant correlation suggests that individual variations in species richness across the plots are not driven by localized fluctuations in abiotic variables, namely soil temperature, soil moisture, air temperature, air humidity, light intensity, and soil pH. Instead, these homogeneous, harsh abiotic parameters particularly the severe soil acidity (pH = 5.1) and nutrient leaching act as a uniform environmental filter. This selective pressure inadvertently creates a distinctive competitive advantage for highly adaptable, generalist invasive plants (Telford et al., 2026). Consequently, this uniform microenvironment enables aggressive non-indigenous species, specifically *Pteridium aquilinum* and *Imperata cylindrica*, to effectively overrun the savanna ecosystem and displace native floral communities.

Table 3. Spearman's Rank Correlation Results Between Species Richness and Environmental Factors

Environmental Factor	Corelation Coefficient (r _s)	Significance value (p-value)	Interpretation
Air temperature (°C)	-0.216	0.251	Not Significant (Negative, weak)
Air humidity (%)	-0.151	0.426	Not Significant (Negative, very weak)
Soil temperature (°C)	0.038	0.842	Not Significant (Positive, very weak)
Soil moisture (%)	0.164	0.388	Not Significant (Positive, very weak)
pH level	0.113	0.552	Not Significant (Positive, very weak)
Light Intensity (Lux)	0.273	0.145	Not Significant (Positive, weak)
Number of Bacteria (CFU)	0.855	0.003**	Significant (Positive, very strong)
Number of Fungi (CFU)	0.197	0.612	Not Significant (Positive, weak)

**Correlation is significant at the 0.01 level (2-tailed).

Conversely, soil bacterial abundance (CFU) exhibits a highly significant, very strong positive correlation with plant species richness ($r_s = 0.855$, $p = 0.003$; Table 3). This contrasting pattern indicates that under the prevailing uniform physicochemical constraints, discrete variations in plant richness are overridden by biological drivers and microbial-plant feedback loops (van der Putten et al.,

2013; Williams & Hauseman et al., 2014; Bennett & Klironomos, 2019). Specifically, the proliferation of culturable bacteria highlights the pivotal role of plant-growth-promoting rhizobacteria (PGPR) and microbial nutrient mineralization, which directly alleviate acid stress and enhance nutrient uptake for native vegetation (Enagbonma et al., 2023; Gonin et al., 2023). Therefore, investigating plant-microbe interactions and interspecific plant competition is critical for assessing the competitive resilience of endemic flora, such as *Styphelia javanica*, when facing invasive species expansion. Understanding these synergetic biological mechanisms is key to formulating targeted ecological conservation strategies to mitigate the threat of local extinction for endemic species in the Bromo savanna.

Unlike typical low-elevation tropical grasslands, such as the African savannas or Baluran's Bekol savanna, the Bromo savanna displays a distinct ecological profile driven by a unique combination of high-altitude climatic, geomorphological, and floristic attributes (Sutomo et al., 2021). Typical savannas in Africa and East Nusa Tenggara thrive under persistent, high-temperature, lowland conditions (ranging from 25°C to 35°C) and are characterized by pronounced seasonal moisture deficits and low annual precipitation. In sharp contrast, the Bromo savanna is situated in the highlands at elevations exceeding 2,000 meters above sea level, spanning ecoclimatically across the montane to subalpine vegetation zones. This high-altitude topography maintains cool to near-freezing temperatures ranging from 3°C to 18°C. Notably, during the peak of the dry season from July to August, the area undergoes severe radiational cooling that drives temperatures down to 0°C, inducing annual frost events and the crystallization of ice on vegetative surfaces (Marchant, 2010; Sutomo et al., 2021; Baliton et al., 2020).

The edaphic matrix further amplifies this divergence; the soil type in the Bromo savanna is a volcanic Regosol formed from volcanic ash. This soil is composed of coarse sand that is rich in macromineral reserves such as phosphorus and potassium, yet exhibits a high sulfur content due to its proximity to the active crater (Novitasari et al., 2018; Hilyah et al., 2021). This profile differs fundamentally from typical tropical savannas, which are primarily characterized by highly weathered, dense, and nutrient-depleted legacy soils such as red laterites (Mareddy, 2017). Nevertheless, the dominance of the coarse sand fraction within this Regosol substrate significantly impairs its cation exchange capacity, rendering it highly inefficient at retaining essential nutrients. The coarse sandy substrate is characterized by a high volume of dominant macropores interspaced between the soil grains, leading to a markedly low water holding capacity (Jamin et al., 2025). Consequently, precipitation in the Bromo area triggers rapid downward water movement via accelerated infiltration, which actively leaches soluble surface nutrients into the subsoil layers. This high percolation rate and subsequent nutrient loss align with the relatively acidic soil pH recorded across the savanna ecosystem (Table 2).

Under a low pH regime, a high concentration of Hydrogen (H^+) and Aluminium (Al^{3+}) ions dominates the soil system, effectively stripping essential cations like Calcium (Ca^{2+}), Magnesium (Mg^{2+}), and Potassium (K^+) from their structural binding sites. Once displaced, these essential macronutrients remain unbound within the soil solution, rendering them highly susceptible to vertical leaching into deeper subsoil layers (Zama et al., 2022). This severe nutrient depletion via leaching may explain why large woody plants struggle to thrive on the Bromo savanna. Conversely, it favors fast-growing herbaceous species and grasses, enabling them to rapidly intercept dissolved nutrients before they are lost to pluvial leaching (Sukweenandhi, 2025). Evaluating these comprehensive vegetation-environment linkages allows for a precise characterization of community assembly patterns under extreme climatic and edaphic stresses, providing a robust framework for forecasting ecosystem responses to future environmental shifts (Maia et al., 2019).

To definitively validate these biological mechanisms and transition from general management frameworks to specific, actionable conservation interventions, future research in the Bromo savanna must prioritize: 1. multi-season vegetation monitoring to track temporal shifts in invasive dominance; 2. high-resolution fire regime mapping to assess the long-term impact of burning on this unique high-altitude ecosystem; 3. controlled competition experiments between *Styphelia javanica* and encroaching

weeds to assess the competitive resilience of endemic flora when facing invasive species expansion; and 4. Investigating plant-microbe and interspecific interactions to unravel how beneficial soil bacteria modulate plant growth and bolster the resilience of endemic flora against invasive colonization.

CONCLUSION

In conclusion, this study successfully addresses the three primary ecological dimensions of the BTSNP savanna during the dry season. First, regarding plant diversity, a total of 15 plant species were recorded, exhibiting a low-to-moderate ecosystem diversity index ($H' = 1.81$). Second, the community structure is severely imbalanced due to the aggressive expansion of generalist invasive species over 73.38% of the landscape, predominantly composed of *Pteridium aquilinum* with a percentage cover of 40.22% (IVI = 69.44%) and *Imperata cylindrica* with a cover of 33.16% (IVI = 55.08%). Crucially, the dominance of these two invasive taxa directly drives the low-to-moderate diversity state, potentially generating severe ecological consequences that compromise the ecosystem's buffering capacity, heighten its vulnerability to environmental perturbations, and accelerate the competitive displacement of rare native endemics. Third, the relationship with environmental factors indicates that while individual abiotic factors (pH = 5.1) present a uniform environmental stress profile, soil bacterial abundance acts as a critical biological determinant that is highly and significantly coupled with plant species richness, likely driving localized native flora persistence against invasive displacement.

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DECLARATIONS

- Author Contributions** : Author 1: Conceptualisation, Methodology, Writing - Original Draft; Author 2: Formal Analysis, Investigation; Author 3: Formal Analysis, Investigation; Author 4: Formal Analysis, Investigation; Author 5: Review, editing; Author 6: Conceptualisation, Funding Acquisition, Project Administration. All authors have read and approved the final manuscript
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Supplementary

Table 1. Minimal area for vegetation sampling plots

A. Optimum quadrat size

Plot	Plot size (m ²)	Species numbers	Increase in the number of species	
			Number	%
1	1 x 1	1	-	-
2	2 x 2	3	2	66.7
3	3 x 3	4	1	25.0
4	4 x 4	5	1	20.0
5	5 x 5	7	1	14.3
6	10 x 5	7	0	0.0

Table 2. Spearman's Rank Correlation Results Between Species Richness and Environmental Factors

			Sp. numbers	AirTemp
Spearman's rho	Sp. numbers	Correlation Coefficient	1.000	-.216
		Sig. (2-tailed)	.	.251
		N	30	30
	AirTemp	Correlation Coefficient	-.216	1.000
		Sig. (2-tailed)	.251	.
		N	30	30
			Sp. numbers	AirMoist
Spearman's rho	Sp. numbers	Correlation Coefficient	1.000	-.151
		Sig. (2-tailed)	.	.426
		N	30	30
	AirMoist	Correlation Coefficient	-.151	1.000
		Sig. (2-tailed)	.426	.
		N	30	30
			Sp. numbers	SoilTemp
Spearman's rho	Sp. numbers	Correlation Coefficient	1.000	.038
		Sig. (2-tailed)	.	.842
		N	30	30
	SoilTemp	Correlation Coefficient	.038	1.000
		Sig. (2-tailed)	.842	.
		N	30	30
			Sp. numbers	SoilMoist
Spearman's rho	Sp. numbers	Correlation Coefficient	1.000	.164
		Sig. (2-tailed)	.	.388
		N	30	30
	SoilMoist	Correlation Coefficient	.164	1.000
		Sig. (2-tailed)	.388	.
		N	30	30
			Sp. numbers	pH
Spearman's rho	Sp. numbers	Correlation Coefficient	1.000	.113
		Sig. (2-tailed)	.	.552
		N	30	30
	pH	Correlation Coefficient	.113	1.000
		Sig. (2-tailed)	.552	.
		N	30	30
			Sp. numbers	LightInt
Spearman's rho	Sp. numbers	Correlation Coefficient	1.000	.273
		Sig. (2-tailed)	.	.145
		N	30	30
	LightInt	Correlation Coefficient	.273	1.000

	Sig. (2-tailed)	.145	.
	N	30	30

			Sp. numbers	Bacteria
Spearman's rho	Sp.numbers	Correlation Coefficient	1.000	.855**
		Sig. (2-tailed)	.	.003
		N	30	9
	Bacteria	Correlation Coefficient	.855**	1.000
		Sig. (2-tailed)	.003	.
		N	9	9

**. Correlation is significant at the 0.01 level (2-tailed).

			Sp. numbers	Fungi
Spearman's rho	Sp. numbers	Correlation Coefficient	1.000	.197
		Sig. (2-tailed)	.	.612
		N	30	9
	Fungi	Correlation Coefficient	.197	1.000
		Sig. (2-tailed)	.612	.
		N	9	9