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Diversity and microclimatic patterns of vascular plant communities in cave-associated karst microhabitats of Ngantap Cave, Central Java, Indonesia

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Abstract. *Paramesti H, Sheliana MS, Hapsari M, Hasan MT, Susatio R, Jumari, Suharno, Setiawan AD. 2025. Diversity and microclimatic patterns of vascular plant communities in cave-associated karst microhabitats of Ngantap Cave, Central Java, Indonesia. Intl J Trop Drylands 9: 169-180.* Karst ecosystems are characterized by strong environmental heterogeneity driven by limestone geomorphology, shallow soils, and localized microclimatic variation. Within these systems, caves play an important role in shaping surrounding terrestrial habitats by generating gradients in light availability, humidity, and air movement. Despite their ecological significance, vegetation associated with cave-related microhabitats outside the cave interior remains poorly documented in tropical karst regions, including Indonesia. This study examines vascular plant communities associated with cave-related microhabitats around Ngantap Cave, Wonogiri District, Central Java, Indonesia, part of the Gunung Sewu UNESCO Global Geopark. Vegetation sampling was conducted using line transects across three cave-associated microhabitat zones: entrance, cliff, and twilight. A total area of 1,800 m² was surveyed, and all vascular plant individuals were recorded and classified by species, family, growth form, and origin status (native, introduced, cultivated). Microclimatic parameters, including air temperature, relative humidity, light intensity, and wind speed, were measured to characterize environmental gradients among zones. Community structure was analyzed using Shannon–Wiener diversity, Simpson dominance, and Pielou evenness indices within a descriptive–comparative framework. A total of 41 vascular plant species belonging to 22 families and comprising 1,736 individuals were recorded. Herbaceous species and ferns dominated cave-associated assemblages, whereas shrubs and small trees were less frequent, and large canopy trees were absent. Species richness and diversity were highest in the entrance zone and declined toward the twilight zone, which supported only a limited number of shade- and humidity-tolerant taxa. Microclimatic conditions exhibited clear and directional gradients, with increasing relative humidity and decreasing light intensity and air movement from the entrance to the twilight zone. Introduced and cultivated species were present but largely confined to entrance areas, reflecting historical tourism-related activities rather than ongoing biological invasion. These findings demonstrate that cave-associated microhabitats support distinct plant communities structured by fine-scale environmental filtering and provide baseline ecological information essential for conserving microhabitat diversity in tropical karst ecosystems.

Keywords: Cave-associated habitat, karst ecosystem, microclimate, vascular plants, vegetation zonation

INTRODUCTION

Karst ecosystems are characterized by highly heterogeneous geomorphology, shallow and discontinuous soils, and strong limitations in water and nutrient availability, making them among the most environmentally constrained terrestrial systems in the tropics (Ford and Williams 2007; Goldscheider and Drew 2007). Limestone dissolution processes generate complex landforms, including cliffs, sinkholes, fissures, and caves, resulting in pronounced spatial variability in substrate stability, moisture retention, and light availability over short distances. This extreme heterogeneity creates sharp ecological gradients at fine spatial scales and imposes strong environmental filters on plant establishment and persistence, often producing distinctive vegetation structures and specialized plant assemblages (Clements et al. 2006; White et al. 2019; Aprilia et al. 2021).

Caves constitute a critical component of karst systems not only as subterranean habitats but also as drivers of localized microclimatic gradients in their surrounding environments. Cave entrances and adjacent limestone surfaces modify air circulation, humidity regimes, and solar radiation, creating transitions from exposed and thermally variable conditions to shaded and persistently humid microhabitats (Badino 2010; Culver and Pipan 2014). These cave-induced gradients frequently extend beyond the cave interior and influence nearby terrestrial habitats that remain functionally linked to the cave system despite not being fully aphotic.

Areas surrounding cave entrances therefore function as ecological transition zones between surface karst landscapes and subterranean environments. Compared with open karst terrain, cave-associated microhabitats often exhibit reduced temperature fluctuations, higher relative humidity, lower light availability, and limited air movement (Badino 2010). Such conditions generate environments that differ markedly from both exposed karst surfaces and true cave interiors, potentially supporting distinct plant assemblages shaped primarily by microclimatic filtering rather than by broader landscape-scale processes. Despite this ecological significance, vegetation associated with cave-related microhabitats outside the cave interior remains poorly documented in tropical karst regions, particularly in Southeast Asia.

Vegetation patterns in tropical karst landscapes are generally shaped by edaphic stress, water scarcity, and the physical instability of limestone substrates. Exposed karst areas are commonly dominated by drought-tolerant trees, shrubs, and climbers, whereas herbs and ferns occupy rock crevices, shaded surfaces, and small soil pockets where moisture availability is relatively higher (Clements et al. 2006; Huang et al. 2022). Structural heterogeneity is a defining feature of karst vegetation, with sharp contrasts among open hills, cliff faces, and sheltered depressions occurring at very fine spatial scales.

Vascular plants inhabiting karst environments exhibit a range of morphological and physiological adaptations, including reduced stature, clonal growth, shade tolerance, and efficient water-use strategies (Porembski and Barthlott 2000; Huang et al. 2022). Ferns and members of the family Araceae are particularly associated with humid and shaded karst microhabitats, where stable moisture availability and reduced irradiance favor their growth (Parris et al. 2010). Climbers and epiphytes further contribute to vegetation complexity by exploiting vertical rock surfaces and existing vegetation, thereby enhancing habitat heterogeneity in limestone landscapes.

Vegetation associated with cave surroundings differs markedly from that of open karst landscapes. While exposed karst habitats are typically dominated by woody species adapted to high irradiance and seasonal drought, cave-associated microhabitats tend to support herbaceous- and fern-rich assemblages that benefit from reduced environmental stress and more stable microclimatic conditions (Poulson and White 1969; Culver and Pipan 2019). These contrasts highlight the ecological importance of cave-associated habitats as distinct components within karst vegetation mosaics rather than marginal extensions of surrounding landscapes.

Indonesia hosts extensive tropical karst landscapes across Java, Sulawesi, and eastern Indonesia, with the Gunung Sewu region of southern Java recognized as a UNESCO Global Geopark. Previous vegetation studies in Gunung Sewu and adjacent areas have largely focused on floristic inventories, forest structure, or land-use impacts at landscape scales (Whitten et al. 1996; Supriatna et al. 2017). Studies conducted in Pacitan, Gunungkidul, and Kebumen document karst flora diversity but generally emphasize open karst hills, forest remnants, or land-use gradients rather than cave-associated microhabitats. Consequently, fine-scale vegetation patterns linked to cave-related microhabitats remain poorly understood in Indonesia, particularly in the Wonogiri sector of the Gunung Sewu karst, where cave surroundings such as those of Ngantap Cave have received little focused scientific attention.

This study provides the first microhabitat-scale assessment of vascular vegetation associated with cave environments outside the cave interior in the Wonogiri sector of the Gunung Sewu karst, Central Java, Indonesia. The study documents species composition and growth-form structure, compares diversity and dominance among entrance, cliff, and twilight zones, and examines vegetation–microclimate relationships using a descriptive approach. The findings supply baseline ecological data that enhance understanding of karst ecosystem complexity and inform conservation and management of cave-associated microhabitat diversity. It is hypothesized that plant species richness, diversity, and growth-form composition decline from the cave entrance toward cliff and twilight zones in response to decreasing light availability and increasing humidity, resulting in distinct microhabitat-specific assemblages.

MATERIALS AND METHODS

Study area

The study was conducted in the surroundings of Ngantap Cave, Wonogiri District, Central Java, Indonesia (8° 04.8515' S, 110° 54.2506' E). Administratively, the site is located within the southern karst belt of Central Java, which forms part of the Gunung Sewu karst region. Geographically, this area lies within the tropical monsoon climate zone, characterized by distinct wet and dry seasons that strongly influence vegetation dynamics and microclimatic conditions.

Ngantap Cave is situated within the Gunung Sewu UNESCO Global Geopark, a landscape recognized for its extensive limestone formations, high geodiversity, and ecological significance. The karst system in this region is dominated by limestone hills, cliffs, sinkholes, and subterranean drainage networks formed through long-term dissolution processes (Ford and Williams 2007). These geomorphological features create strong environmental heterogeneity, particularly in terms of substrate depth, surface stability, and water availability, which in turn shape vegetation structure and species distribution.

The immediate surroundings of Ngantap Cave are characterized by steep limestone cliffs, shaded rock faces, and narrow entrance areas, with minimal development of flat terrain. Historically, the cave and its surroundings were used as a local tourism site; however, declining visitor numbers have resulted in limited maintenance and reduced human disturbance in recent years. This condition has allowed semi-natural vegetation to persist and regenerate around the cave system, including both native species and cultivated or introduced plants associated with earlier tourism activities. The combination of karst geomorphology and reduced anthropogenic pressure makes the Ngantap Cave area suitable for examining vascular plant communities associated with cave-related microhabitats (Figure 1).

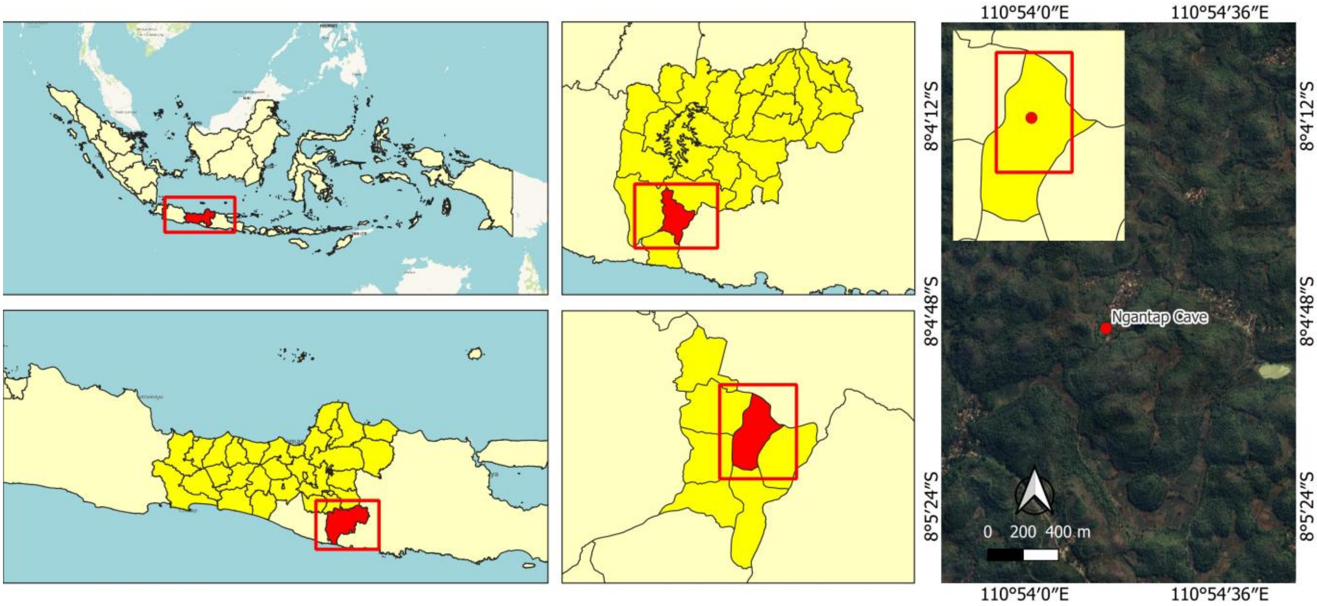

Figure 1. Research location map of Ngantap Cave and surrounding karst microhabitats in Central Java, Indonesia

Cave-associated microhabitat zoning

Vegetation sampling was organized according to cave-associated microhabitat zones defined based on geomorphological position, light availability, and microclimatic conditions. Three zones were distinguished: the entrance zone, the cliff zone, and the twilight (humid) zone. This zonation follows ecological principles commonly applied in cave and karst studies to capture environmental gradients extending outward from cave openings (Badino 2010; Culver and Pipan 2014), with emphasis on habitats that remain functionally influenced by cave morphology and airflow but are located outside the cave interior.

The entrance zone refers to areas directly adjacent to the cave opening that receive partial to full sunlight for part of the day. These areas experience greater temperature fluctuation, higher light intensity, and lower relative humidity compared to more cave-influenced zones, while still being affected by air exchange with the cave interior. The cliff zone comprises vertical or steeply inclined limestone surfaces surrounding the cave, characterized by shallow or absent soil, high surface roughness, and intermediate light conditions dominated by diffuse or reflected radiation due to microtopographic shading. Vegetation in this zone is typically restricted to rock crevices and small soil pockets, resulting in a dominance of stress-tolerant herbs, ferns, and climbers.

The twilight (humid) zone is defined as shaded areas located further from direct sunlight but still outside the cave interior. Within the context of this study, the twilight zone represents the most light-limited and humid microhabitat recorded, characterized by very low irradiance, minimal air movement, and relatively stable microclimatic conditions. These areas receive weak, diffused light and maintain high relative humidity due to reduced evaporation and close functional linkage to cave airflow. Such conditions favor shade-tolerant vascular plants, particularly ferns and members of Araceae, which are commonly associated with moist karst microhabitats.

Importantly, this study does not include open karst plains, agricultural land, or flat forested areas located away from the cave system. By restricting sampling to these three cave-associated zones, the analysis explicitly targets microhabitats that are environmentally filtered by cave-related geomorphology and microclimate, rather than broader karst landscapes influenced primarily by surface processes.

Vegetation sampling design

Vegetation sampling was conducted using a line transect method to capture fine-scale variation in species composition across cave-associated microhabitats. This method is widely applied in heterogeneous environments such as karst landscapes, where vegetation distribution is strongly influenced by microtopography and substrate discontinuity (Kent 2012). Transects were established separately within each defined microhabitat zone (entrance, cliff, and twilight) to ensure balanced spatial representation.

In each zone, three line transects measuring 50 m × 4 m were laid parallel to local geomorphological features, resulting in a total of nine transects. The total sampled area covered 1,800 m². Transect placement avoided overlap and followed accessible natural contours without modifying the substrate. All vascular plant individuals occurring within transect boundaries were recorded, regardless of size class, to capture the full spectrum of growth forms present in cave-associated habitats.

Individual plants were defined as distinct, physically separated entities. For clonal or creeping species, individuals were counted based on visible ramets when separation was clear in the field. Each recorded species was classified into growth form categories, including fern, herb, shrub, tree, climber, bamboo, and orchid, based on field-observed habitus. This classification emphasizes functional structure rather than strict life-form schemes, allowing direct comparison among microhabitat zones (Table 1).

Species identification was carried out through a combination of field observation and post-field verification. Preliminary identification was conducted in situ using regional floras, particularly *Flora of Java* (Backer and Bakhuizen van den Brink 1963-1968), supplemented by taxonomic references relevant to ferns and flowering plants of Java and Malesia (Holttum 1954; Piggott 1988; Parris et al. 2010). Scientific names were subsequently verified using authoritative online databases, including Plants of the World Online (POWO 2026, Royal Botanic Gardens, Kew; https://powo.science.kew.org) and the International Plant Names Index (IPNI 2026; https://www.ipni.org), to ensure nomenclatural consistency. Although accepted names from POWO and IPNI were consulted, several species are presented using names commonly applied in regional floristic and ecological studies of Java to ensure consistency with field identification and local literature. Final identifications were confirmed by cross-checking diagnostic morphological characters with published descriptions and verified images from these sources.

Microclimatic measurements

Microclimatic conditions were measured to characterize environmental variation among cave-associated microhabitat zones and to support a descriptive interpretation of vegetation patterns. Four key parameters were recorded: air temperature, Relative Humidity (RH), light intensity, and wind speed. These variables are commonly used to describe microclimatic gradients in karst and cave-related environments, as they directly influence plant physiological processes and habitat suitability (Badino 2010; Culver and Pipan 2014).

Measurements were conducted using portable field instruments. Air temperature and relative humidity were recorded with a digital thermo-hygrometer, light intensity was measured using a handheld lux meter, and wind speed was assessed using a portable anemometer. All instruments were calibrated according to manufacturer specifications prior to field deployment. Within each microhabitat zone, measurements were taken at multiple representative points along every vegetation transect to ensure adequate spatial coverage and direct correspondence between vegetation data and environmental conditions.

Data collection was carried out during daytime hours (approximately mid-morning to early afternoon) under comparable weather conditions to minimize the influence of short-term climatic variability. Along each transect, microclimatic readings were recorded at regular intervals, with sensors positioned at approximately 1 m above ground level to represent conditions experienced by the understory vegetation. For each microhabitat zone, measurements were conducted on the same sampling days to allow direct comparison among zones.

All measurements obtained from multiple points and transects within each zone were pooled and averaged to derive mean microclimatic values for the entrance, cliff, and twilight zones. These mean values were subsequently used to summarize environmental gradients and to support descriptive analyses of vegetation–microclimate relationships. Given the exploratory scope of the study and the limited spatial extent of the sampling area, microclimatic data were not subjected to inferential statistical testing but were interpreted comparatively among zones.

Data analysis

Vegetation data were analyzed to describe species diversity, dominance, and community structure across cave-associated microhabitat zones. Species abundance data obtained from transects were used to calculate standard diversity indices, including the Shannon–Wiener diversity index (H′), Simpson dominance index (D), and Pielou's evenness index (E). These indices are widely applied in vegetation ecology to summarize community complexity, dominance patterns, and the distribution of individuals among species (Magurran 2004; Kent 2012).

The Shannon–Wiener diversity index (H′) was calculated to represent overall species diversity by incorporating both species richness and relative abundance. Simpson's dominance index (D) was used to assess the extent to which communities were dominated by one or a few species, with higher values indicating greater dominance. Pielou's evenness index (E) was calculated to evaluate how evenly individuals were distributed among recorded species within each microhabitat zone. All indices were calculated separately for the entrance, cliff, and twilight zones to enable zone-specific comparison of community structure.

Interpretation of diversity indices followed commonly accepted ecological guidelines, where higher H′ values indicate greater diversity, higher D values reflect stronger dominance, and E values approaching 1 indicate more even species distributions (Magurran 2004). Rather than applying rigid categorical thresholds, index values were interpreted comparatively among zones to highlight relative differences in community structure.

Given the limited spatial extent of the study area, the small number of transects per zone, and the strong microhabitat-specific filtering inherent to cave-associated karst environments, the analysis adopted a descriptive–comparative approach without inferential statistical testing. Under such conditions, inferential statistics may provide limited ecological meaning and risk overstating generality. Accordingly, diversity indices and microclimatic data were used to support qualitative and comparative interpretation of vegetation patterns across cave-associated zones, emphasizing baseline documentation and ecological plausibility rather than hypothesis testing.

RESULTS AND DISCUSSION

Species composition and structural attributes

A total of 41 vascular plant species belonging to 22 families, comprising 1,736 recorded individuals, were documented across cave-associated microhabitat zones around Ngantap Cave (Table 1). Species richness and abundance were unevenly distributed among zones, with the entrance zone supporting the highest number of individuals, followed by the cliff zone, while the twilight zone contained only a very limited number of species and individuals.

A limited number of plant families taxonomically dominated the recorded flora. Asteraceae was the most species-rich family, contributing several herbaceous taxa commonly associated with disturbed or semi-open habitats. Fern families, particularly Thelypteridaceae, Pteridaceae, and Blechnaceae, were also well represented and were common in shaded and humid microhabitats associated with the cave system. Araceae contributed several species with creeping or climbing growth forms, while Fabaceae and Euphorbiaceae were represented by both herbaceous and woody taxa (Table 1).

Table 1. Species composition, family, growth form, and status

Species	Family	Growth form	Status
Celtis timorensis Span.	Cannabaceae	Tree	Native
Epipremnum pinnatum (L.) Engl.	Araceae	Climber	Native
Ficus callosa Willd.	Moraceae	Tree	Native
Thelypteris pozoi (C.Chr.) Morton	Thelypteridaceae	Fern	Native
Adiantum capillus-veneris L.	Pteridaceae	Fern	Native
Christella dentata (Forssk.) Brownsey & Jermy	Thelypteridaceae	Fern	Native
Christella parasitica (L.) H.Lév.	Thelypteridaceae	Fern	Native
Homalomena rubescens Kunth	Araceae	Herb	Native
Pilea angulata (J.R.Forst. & G.Forst.) Blume	Urticaceae	Herb	Native
Schismatoglottis calyptrata (Roxb.) Zoll. & Moritzi	Araceae	Herb	Native
Abrus precatorius L.	Fabaceae	Climber	Native
Acalypha brachystachya Hornem.	Euphorbiaceae	Herb	Native
Adiantum raddianum C.Presl	Pteridaceae	Fern	Introduced
Ageratum conyzoides L.	Asteraceae	Herb	Introduced
Ageratum houstonianum Mill.	Asteraceae	Herb	Introduced
Amphicarpaea bracteata (L.) Fernald	Fabaceae	Climber	Introduced
Bambusa vulgaris var. *vittata* (Aiton) A.Chev.	Poaceae	Bamboo	Cultivated
Blechnum orientale L.	Blechnaceae	Fern	Native
Caladium bicolor (Aiton) Vent.	Araceae	Herb	Cultivated
Casearia grewiaefolia Vent.	Salicaceae	Tree	Native
Centella asiatica (L.) Urb.	Apiaceae	Herb	Native
Christella normalis (C.Chr.) Holttum	Thelypteridaceae	Fern	Native
Chromolaena odorata (L.) R.M.King & H.Rob.	Asteraceae	Shrub	Introduced
Clidemia hirta (L.) D.Don	Melastomataceae	Shrub	Introduced
Codiaeum variegatum (L.) Rumph. ex A.Juss.	Euphorbiaceae	Shrub	Cultivated
Cordyline fruticosa (L.) A.Chev.	Asparagaceae	Shrub	Cultivated
Crassocephalum crepidioides (Benth.) S.Moore	Asteraceae	Herb	Introduced
Crinum asiaticum L.	Amaryllidaceae	Herb	Native
Davallia denticulata (Burm.f.) Mett.	Davalliaceae	Fern	Native
Dendrobium discolor var. *bromfieldii* (F.Muell.)	Orchidaceae	Epiphyte	Cultivated
Desmodium triflorum (L.) DC.	Fabaceae	Herb	Native
Diplazium esculentum (Retz.) Sw.	Athyriaceae	Fern	Native
Duranta erecta L.	Verbenaceae	Shrub	Cultivated
Litsea glutinosa (Lour.) C.B.Rob.	Lauraceae	Tree	Native
Manihot esculenta Crantz	Euphorbiaceae	Shrub	Cultivated
Melochia villosissima Blume	Malvaceae	Shrub	Native
Phytolacca acinosa Roxb.	Phytolaccaceae	Herb	Introduced
Polyalthia longifolia (Sonn.) Thwaites	Annonaceae	Tree	Cultivated
Samanea saman (Jacq.) Merr.	Fabaceae	Tree	Introduced
Synedrella nodiflora (L.) Gaertn.	Asteraceae	Herb	Introduced
Youngia japonica (L.) DC.	Asteraceae	Herb	Introduced

Note: Species nomenclature follows commonly used names in regional floristic studies and was verified against Plants of the World Online (POWO) and the International Plant Names Index (IPNI). Growth form classification is based on field-observed habitus, and species status (native, introduced, cultivated) follows regional floras and common usage in Java, Indonesia

In terms of growth form, herbaceous species constituted the largest proportion of recorded taxa, followed by ferns. Shrubs and small trees were present but comparatively less abundant, and large canopy tree species were absent from all sampling zones. Climbers, including both woody and herbaceous forms, contributed a smaller but ecologically notable component of the vegetation. Orchid representation was limited to a single cultivated epiphytic taxon. This structural pattern indicates a community dominated by low-stature vegetation adapted to shallow soils, rock crevices, and shaded limestone surfaces.

Species status classification revealed a mixed assemblage of native, introduced, and cultivated plants (Table 1). Native species accounted for the largest proportion of taxa and individuals, particularly among ferns and shade-tolerant herbs. Introduced species were mainly herbaceous taxa commonly associated with anthropogenic disturbance, whereas cultivated species consisted primarily of ornamental or food plants likely originating from earlier tourism-related planting or nearby human activity. Despite their presence, cultivated taxa contributed only a minor proportion of total abundance.

Spatially, most species were concentrated in the entrance and cliff zones, where higher light availability and substrate heterogeneity allowed the coexistence of multiple growth forms. In contrast, the twilight zone supported very few species and individuals, reflecting its low light intensity and persistently humid conditions. Representative species illustrating the range of growth forms and microhabitat associations observed in the study area are shown in Figure 2.

Spatial distribution of species across microhabitat zones

The spatial distribution of vascular plant species around Ngantap Cave showed clear variation among the three cave-associated microhabitat zones: entrance, cliff, and twilight (Table 2; Figure 3). Species richness and individual abundance were strongly concentrated in the entrance zone, which supported 31 species and 1,502 individuals, representing the majority of the recorded flora. This zone harbored a heterogeneous assemblage of herbs, ferns, shrubs, climbers, and small trees, coinciding with relatively higher light availability and greater substrate heterogeneity.

The cliff zone exhibited a distinct but substantially less diverse assemblage compared to the entrance zone. Only 6 species comprising 226 individuals were recorded in this zone. Species occurring here were largely restricted to taxa capable of establishing on steep limestone surfaces, rock crevices, and shallow soil pockets. Ferns and shade-tolerant herbs dominated the assemblage, while woody tree species were absent. Several species abundant in the entrance zone were not recorded on cliffs, indicating strong microhabitat filtering associated with substrate instability and limited soil development (Table 2).

In contrast, the twilight zone supported a highly restricted plant community. This zone contained only 4 species and 9 individuals in total. All recorded taxa were shade-tolerant and associated with persistently humid conditions, and no woody species were observed. Species richness in the twilight zone was markedly lower than in both the entrance and cliff zones, reflecting the combined constraints of low light availability and stable, humid microclimatic conditions.

Patterns of species presence and absence further emphasized differentiation among zones. Many herbaceous and introduced species were confined exclusively to the entrance zone and were absent from both the cliff and twilight zones. Conversely, a subset of fern species showed broader ecological tolerance, occurring in both entrance and cliff zones, although with marked differences in abundance. Overlap in species composition between the cliff and twilight zones was minimal, highlighting the distinct environmental conditions characterizing these habitats.

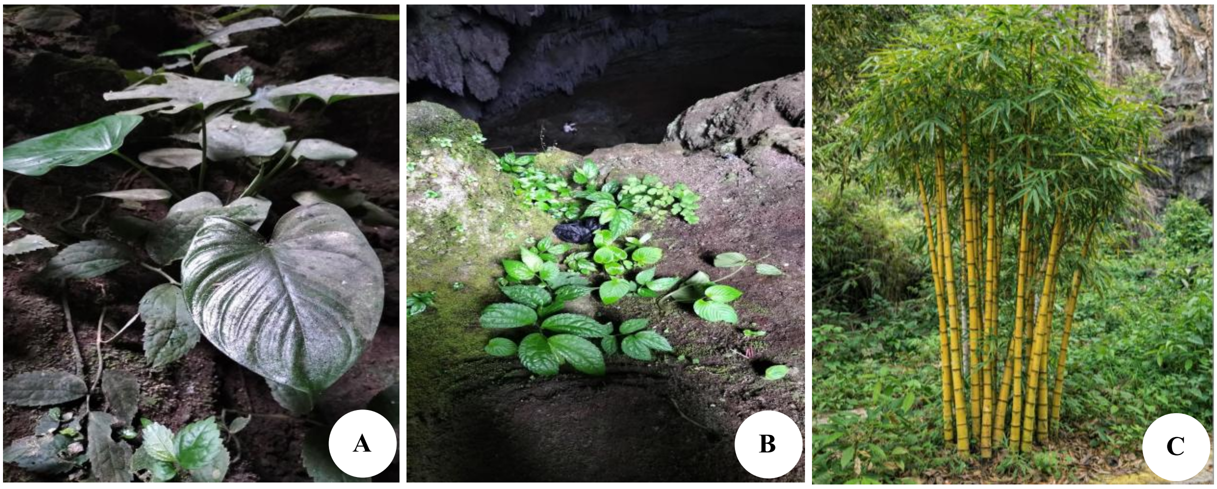

Figure 2. Representative vascular plant species across cave-associated microhabitat zones around Ngantap Cave, Wonogiri, Central Java, Indonesia. A. *Epipremnum pinnatum* in the twilight zone, B. *Pilea angulata* along the cliff zone, and C. *Bambusa vulgaris* var. *vittata* in the entrance zone

The entrance zone functioned as the primary reservoir of species richness within the cave-associated system, while the cliff zone represented a more specialized habitat supporting a reduced but distinctive assemblage. The twilight zone constituted the most environmentally restrictive microhabitat, supporting only a small subset of the regional species pool. Differences in species richness among zones are summarized in Figure 3, while detailed abundance data for each species across zones are presented in Table 2.

Diversity and dominance patterns among zones

Patterns of species diversity and dominance varied distinctly among the three cave-associated microhabitat zones around Ngantap Cave (Table 3). Quantitative indices revealed strong contrasts in community structure, reflecting differences in species richness, relative abundance, and the distribution of individuals among recorded species.

The entrance zone exhibited the highest Shannon–Wiener diversity index (H′ = 3.242), indicating substantially greater species diversity compared to the other zones. This zone also showed the lowest Simpson dominance value (D = 0.045), suggesting weak dominance and the absence of a single overwhelmingly abundant taxon. The high Pielou evenness value (E = 0.944) further indicates that individuals were relatively evenly distributed among species. Together, these values characterize the entrance zone as the most structurally complex and balanced plant community within the cave-associated system.

In contrast, the cliff zone displayed markedly lower diversity (H′ = 1.421) than the entrance zone. The Simpson dominance index was considerably higher (D = 0.283), indicating increased dominance by a limited number of species. The evenness value (E = 0.793) suggests a moderately uneven distribution of individuals, with several fern and herb taxa accounting for a large proportion of total abundance. These index values indicate stronger microhabitat filtering in the cliff zone, resulting in reduced diversity and increased dominance compared to the entrance zone.

The twilight zone showed the lowest overall diversity (H′ = 1.369), reflecting both low species richness and restricted total abundance. Although Simpson dominance remained relatively high (D = 0.259), the Pielou evenness index was very high (E = 0.987), indicating that the few species present occurred in relatively similar abundances, rather than being dominated by a single species. This combination reflects a simplified community structure shaped primarily by severe environmental constraints, rather than competitive exclusion.

The entrance zone supported the most diverse and structurally balanced plant community, whereas the twilight zone represented the most simplified assemblage characterized by low richness but high evenness among a small number of species. The cliff zone occupied an intermediate position between these two extremes. Diversity and dominance indices summarized in Table 3 provide a quantitative basis for subsequent discussion of ecological filtering and microhabitat specialization in cave-associated karst environments.

Table 2. Species abundance by microhabitat zone

Species	**Zone**		
	Entrance	**Cliff**	**Twilight**
Celtis timorensis	–	–	2
Epipremnum pinnatum	–	–	2
Ficus callosa	–	–	2
Thelypteris pozoi	–	–	3
Adiantum capillus-veneris	–	12	–
Christella dentata	–	60	–
Christella parasitica	–	50	–
Homalomena rubescens	–	5	–
Pilea angulata	–	90	–
Schismatoglottis calyptrata	–	9	–
Abrus precatorius	99	–	–
Acalypha brachystachya	88	–	–
Adiantum raddianum	18	–	–
Ageratum conyzoides	34	–	–
Ageratum houstonianum	19	–	–
Amphicarpaea bracteata	11	–	–
Bambusa vulgaris var. *vittata*	14	–	–
Blechnum orientale	40	–	–
Caladium bicolor	10	–	–
Casearia grewiaefolia	30	–	–
Centella asiatica	130	–	–
Christella normalis	69	–	–
Chromolaena odorata	78	–	–
Clidemia hirta	30	–	–
Codiaeum variegatum	59	–	–
Cordyline fruticosa	26	–	–
Crassocephalum crepidioides	17	–	–
Crinum asiaticum	87	–	–
Davallia denticulata	39	–	–
Dendrobium discolor var. *bromfieldii*	55	–	–
Desmodium triflorum	78	–	–
Diplazium esculentum	78	–	–
Duranta erecta	35	–	–
Litsea glutinosa	14	–	–
Manihot esculenta	56	–	–
Melochia villosissima	55	–	–
Phytolacca acinosa	22	–	–
Polyalthia longifolia	51	–	–
Samanea saman	25	–	–
Synedrella nodiflora	90	–	–
Youngia japonica	45	–	–
Total	1502	226	9

Note: Values indicate the number of individuals recorded per species in each microhabitat zone; "–" denotes absence

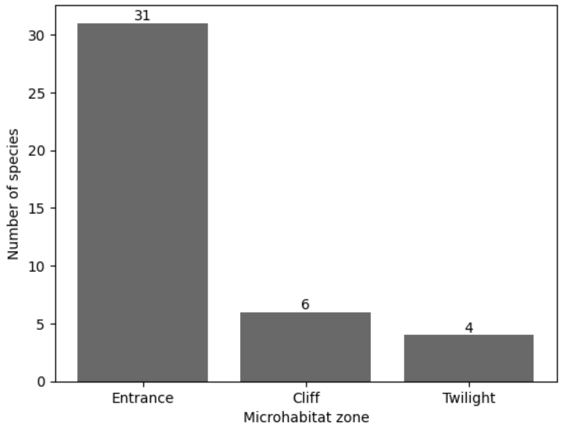

Figure 3. Species richness across cave-associated microhabitat zones

Microclimatic characteristics of cave-associated zones

Microclimatic conditions measured around Ngantap Cave showed clear and consistent differentiation among the entrance, cliff, and twilight zones, reflecting strong environmental gradients within the cave-associated system (Table 4). Variations were evident across all measured parameters, including Relative Humidity (RH), air temperature, light intensity, and wind speed, indicating a progressive transition from exposed and dynamic conditions at the entrance to increasingly shaded, humid, and climatically stable environments toward the twilight zone.

Relative humidity increased along the cave-associated gradient from the entrance zone toward the twilight zone. The entrance zone recorded the lowest mean RH value (76.68%), consistent with greater exposure to solar radiation and higher air movement. The cliff zone exhibited intermediate humidity levels (77.98%), likely reflecting partial shading and reduced evaporation on vertical limestone surfaces. The twilight zone maintained the highest RH (82.56%), indicating persistently humid conditions associated with minimal air circulation and close functional linkage to cave airflow (Table 4).

Air temperature showed only minor variation among zones compared to humidity. The entrance zone recorded the highest mean temperature (29.8°C), corresponding to its greater exposure to direct sunlight. Temperatures in the cliff zone were slightly lower (29.2°C), while the twilight zone exhibited the lowest mean temperature (29.0°C). These small differences indicate effective thermal buffering within cave-associated microhabitats, particularly in shaded and partially enclosed zones.

Light intensity displayed the strongest and most pronounced gradient among all measured variables. The entrance zone received very high light levels (5746.67 lux), reflecting direct exposure to sunlight. Light intensity declined markedly in the cliff zone (1472.50 lux), where illumination was dominated by diffuse and reflected light rather than direct solar radiation. The twilight zone exhibited the lowest light intensity (37.00 lux), representing the most light-limited microhabitat due to strong shading, reduced sky exposure, and proximity to the cave interior. This clear reduction in irradiance from entrance to twilight zone highlights light availability as a primary abiotic gradient structuring cave-associated environment (Figure 4).

Wind speed was generally low across the study area but showed clear spatial variation among zones. The entrance zone experienced the highest mean wind speed (1.10 m/s), consistent with its openness and direct exposure to external airflow. Wind movement decreased sharply in the cliff zone (0.06 m/s) and was effectively absent in the twilight zone (0.00 m/s), reflecting strong sheltering effects of limestone formations and restricted air exchange near the cave interior.

These microclimatic patterns illustrate a coherent and directional shift from exposed, brighter, and more ventilated conditions at the entrance to darker, more humid, and climatically buffered environments in the twilight zone, reflecting a strong microhabitat gradient within the cave-associated landscape.

Table 3. Diversity and dominance indices

Microhabitat zone	Shannon-Wiener (H′)	Simpson dominance (D)	Pielou evenness (E)
Entrance	3.242	0.045	0.944
Cliff	1.421	0.283	0.793
Twilight	1.369	0.259	0.987

Table 4. Abiotic characteristics of cave-associated microhabitat zones

Microhabitat zone	Air temperature (°C)	Relative humidity (%)	Wind speed (m/s)	Light intensity (lux)
Entrance	29.8	76.68	1.10	5746.67
Cliff	29.2	77.98	0.06	1472.50
Twilight	29.0	82.56	0.00	37.00

Note: Values represent mean measurements recorded during the sampling period. Microhabitat zones include the entrance, cliff, and twilight zones surrounding Ngantap Cave, Wonogiri, Central Java, Indonesia

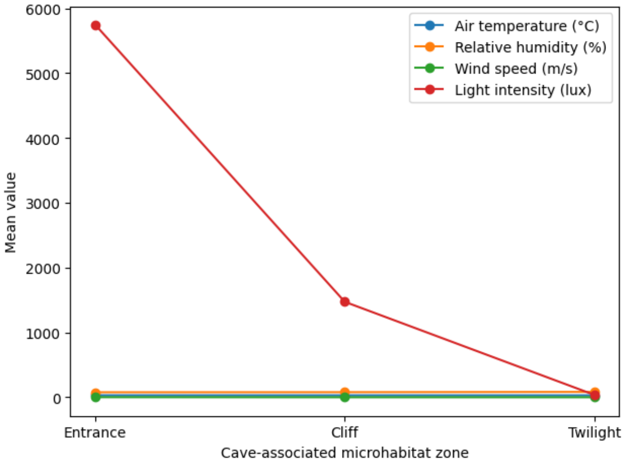

Figure 4. Microclimatic characteristics of cave-associated microhabitat zones (entrance, cliff, and twilight) around Ngantap Cave, Wonogiri, Central Java, Indonesia, based on mean air temperature, relative humidity, wind speed, and light intensity

Discussion

Ecological meaning of species composition and growth forms

The vascular plant communities recorded around Ngantap Cave are characterized by a clear dominance of herbaceous species and ferns, accompanied by a relatively low representation of shrubs and small trees, and the absence of large canopy-forming trees. This growth-form spectrum corresponds closely with the pronounced microhabitat heterogeneity and physical constraints of cave-associated karst environments, where shallow soils, extensive rock exposure, and discontinuous substrates limit the establishment of deep-rooted woody vegetation. Similar structural configurations have been reported from tropical karst systems in which vegetation patterns are governed more strongly by edaphic stress and microtopographic complexity than by successional age or stand development (Porembski and Barthlott 2000; Clements et al. 2006).

The prominence of ferns within the studied assemblages reflects their ecological affinity for shaded, humid, and structurally complex habitats. Ferns are particularly well adapted to limestone environments due to their ability to colonize rock crevices, tolerate thin or absent soil layers, and complete key life stages under low-light conditions. In the Ngantap Cave system, fern dominance was most evident in the cliff and twilight zones, where environmental constraints exclude most woody taxa, allowing pteridophytes to occupy microhabitats that are unsuitable for many seed plants. This pattern aligns with previous observations that ferns often dominate vegetation in humid karst microhabitats characterized by limited irradiance and high substrate instability (Parris et al. 2010; Watkins and Cardelús 2012).

Herbaceous angiosperms also constituted a substantial proportion of the recorded flora, particularly in the entrance zone. Many of these species exhibit flexible life-history strategies, rapid growth, and tolerance to fluctuating microclimatic conditions. Such functional traits are advantageous in ecotonal environments, where light availability, humidity, and disturbance intensity vary over short spatial scales. The entrance zone, functioning as a transition between open karst surfaces and more buffered cave-influenced habitats, therefore supports the coexistence of light-demanding herbs and shade-tolerant taxa, contributing to its comparatively high species richness.

The limited occurrence of shrubs and small trees, together with the complete absence of large canopy-forming species, further highlights the role of vertical habitat structure in shaping vegetation composition. In the study area, steep rock faces, narrow ledges, and unstable substrates restrict rooting depth and mechanical support, thereby constraining the development of tall woody growth forms. Instead, structural complexity is achieved through climbers and scrambling species, which exploit vertical rock surfaces and existing vegetation for support. This form of vertical stratification enhances habitat heterogeneity without leading to closed-canopy formation, a characteristic feature of karst landscapes with rugged topography (Huang et al. 2022).

The observed dominance of low-stature growth forms reflects a vegetation structure finely tuned to the physical and microclimatic conditions of cave-associated karst habitats. Rather than indicating an early or degraded successional stage, this assemblage represents a relatively stable configuration maintained by persistent environmental filtering at the cave–karst interface. The growth-form composition documented in this study, therefore, underscores the ecological importance of microhabitat heterogeneity and vertical structural constraints in shaping plant communities specifically associated with karst cave systems, distinguishing them from vegetation patterns reported in adjacent open karst forests or hill-slope environments.

Microhabitat filtering and zonation around cave systems

The differentiation of vegetation among entrance, cliff, and twilight zones around Ngantap Cave reflects a clear process of microhabitat filtering driven by gradients in light availability, substrate stability, and microclimatic conditions. These gradients do not produce a simple, continuous vegetation transition; instead, they generate discrete ecological compartments, within which only species possessing appropriate functional traits are able to establish and persist. Such compartmentalization is a characteristic feature of cave-associated karst systems, where abrupt changes in physical and microclimatic conditions occur over short spatial distances.

The entrance zone functions as a transitional habitat between open karst surfaces and cave-influenced environments. This zone exhibited the highest species richness and diversity, accommodating a wide range of growth forms, including herbs, ferns, shrubs, climbers, and small trees. The coexistence of multiple growth forms reflects relatively relaxed environmental filtering, resulting from intermediate light levels, moderate humidity, and heterogeneous substrates. Ecotonal environments such as cave entrances are widely recognized as biodiversity hotspots because overlapping environmental conditions allow taxa from adjacent habitat types to coexist (Poulson and White 1969; Culver and Pipan 2019). The patterns observed at Ngantap Cave are consistent with this framework, identifying the entrance zone as a key reservoir of plant diversity within the cave-associated system.

In contrast, the cliff and twilight zones function as more strongly filtered habitats. The cliff zone is characterized by steep limestone surfaces, shallow or absent soils, and high mechanical instability, which severely restricts plant establishment. Only species capable of anchoring within rock crevices, tolerating episodic water limitation, or exploiting vertical substrates were able to persist in this zone. Ferns and selected herbaceous taxa dominated the assemblage, reflecting their tolerance of physical stress and substrate discontinuity. Comparable vegetation patterns have been reported from karst cliffs elsewhere in the Gunung Sewu region, where plant communities are typically sparse and composed primarily of stress-tolerant growth forms (Porembski and Barthlott 2000; Parris et al. 2010).

The twilight zone represents the most strongly filtered microhabitat. It is characterized by very low light availability, high relative humidity, and minimal air movement, conditions that impose severe physiological constraints on vascular plants. Species richness and abundance were lowest in this zone, and community composition was restricted to a small subset of shade-tolerant taxa. This sharp reduction in diversity with declining light availability conforms closely to classical cave ecology models, which emphasize light as the primary limiting factor controlling biological organization near cave entrances (Poulson and White 1969; Badino 2010). Although no obligate cave-adapted vascular plants were recorded, the twilight zone nevertheless excludes most surface vegetation through persistent microclimatic filtering.

Comparisons with previous vegetation studies in the Gunung Sewu karst indicate that such fine-scale zonation is frequently overlooked. Most regional studies focus on open karst forests, slopes, or hilltops, where deeper soils permit the development of woody vegetation and canopy-forming trees. The Ngantap Cave system demonstrates that cave-associated microhabitats support plant assemblages that are structurally and compositionally distinct from surrounding karst landscapes, even over very short spatial scales. These findings underscore the importance of recognizing caves and their immediate surroundings as functionally unique ecological units within karst ecosystems, rather than treating them as marginal extensions of adjacent habitats.

Vegetation–microclimate relationships (descriptive)

Patterns of vegetation distribution around Ngantap Cave showed a close correspondence with measured microclimatic gradients, particularly relative humidity and light availability. Rather than implying direct causal relationships, these patterns represent functional alignment between plant growth forms and prevailing environmental conditions across cave-associated zones, consistent with descriptive ecological inference. The cave-associated microhabitats exhibited a clear and directional microclimatic gradient, characterized by decreasing light intensity and wind speed and increasing relative humidity from the entrance toward the twilight zone. Such correspondence is characteristic of karst systems, where microclimate operates as a dominant ecological filter shaping plant assemblages at fine spatial scales (Badino 2010; Culver and Pipan 2019).

Herbaceous species were most abundant in the entrance zone, where light intensity was highest, and relative humidity was lower than in the cliff and twilight zones. Many herbaceous taxa recorded in this zone exhibit flexible physiological strategies that allow tolerance of fluctuating irradiance and moisture regimes. These traits facilitate rapid growth and persistence in transitional environments, where microclimatic conditions vary both diurnally and seasonally. Consequently, the entrance zone supports a mixed assemblage of light-demanding and moderately shade-tolerant species, reinforcing its role as a microclimatic ecotone between exposed karst surfaces and cave-influenced habitats.

Ferns exhibited a pronounced affinity for zones characterized by higher relative humidity and lower light availability, particularly the cliff and twilight zones. Fern life cycles depend strongly on moist microenvironments for spore germination and gametophyte development, making them reliable indicators of humidity gradients. Their prevalence on shaded limestone crevices and persistently humid rock surfaces around Ngantap Cave is consistent with previous studies emphasizing the importance of stable moisture availability for pteridophyte persistence in karst landscapes (Parris et al. 2010; Watkins and Cardelús 2012). The increasing dominance of ferns from the cliff zone to the twilight zone reflects the combined influence of high humidity, low irradiance, and minimal air movement, particularly given the minimal temperature differences observed among zones.

Members of the family Araceae also showed a strong association with humid and shaded microhabitats. Araceous species typically possess broad leaves, thin cuticles, and high transpiration capacity, traits that are advantageous under conditions of high humidity and low evaporative demand. Their concentration on the cliff and especially the twilight zone corresponds closely with the most humid and light-limited conditions recorded in the study area, reinforcing their suitability as indicators of cave-influenced microhabitats. Comparable associations between Araceae and humid karst environments have been reported from other tropical limestone regions (Boyce et al. 2025).

In contrast, woody growth forms were largely restricted to zones with relatively higher light availability and more stable rooting substrates. The scarcity of shrubs and the absence of large trees in shaded and humid zones emphasize the combined constraints imposed by low irradiance, shallow soils, and limited mechanical stability. Reduced light availability limits photosynthetic potential, while persistently humid conditions and discontinuous substrates restrict structural support for woody stems, thereby constraining the establishment of tall growth forms in cliff and twilight microhabitats.

The vegetation–microclimate relationships documented in this study underscore the central role of increasing humidity, decreasing light availability, and reduced air movement in structuring cave-associated plant communities. Growth form distribution reflects adaptive responses to fine-scale microclimatic filtering rather than successional trajectories, highlighting the ecological importance of cave-associated microhabitats as distinct and environmentally restrictive components of tropical karst ecosystems.

Introduced and cultivated species in abandoned cave-tourism areas

The occurrence of introduced and cultivated plant species within cave-associated microhabitats around Ngantap Cave is best interpreted as a legacy of historical land use rather than as evidence of ongoing biological invasion. Several recorded taxa are widely used as ornamental or utilitarian plants in Java and are likely remnants of past planting associated with tourism facilities, site landscaping, or nearby human settlements. Their presence therefore reflects socio-ecological history and past management practices, rather than autonomous spread driven by invasive dynamics.

Abandoned or weakly managed tourism sites often function as transitional or semi-natural landscapes, where planted species persist alongside native vegetation under reduced disturbance and maintenance. In the Ngantap Cave area, declining visitor activity has resulted in minimal active management, allowing cultivated plants to survive and coexist locally with native taxa without further human intervention. Comparable patterns have been documented in abandoned recreational and cultural sites, where ornamental or planted species remain embedded within regenerating vegetation matrices (Hobbs et al. 2009; Kowarik 2011).

Spatially, introduced and cultivated species were largely restricted to the entrance zone, where light availability, substrate depth, and accessibility are more favorable for their establishment. These taxa were absent or extremely rare in the cliff and twilight zones, indicating strong environmental filtering that limits their persistence beyond relatively open and accessible microhabitats. Such spatial confinement suggests that these species are not actively expanding into cave-associated environments but are instead constrained by microclimatic conditions, substrate instability, and low light availability.

Importantly, none of the introduced or cultivated species exhibited dominance patterns characteristic of invasive behavior, such as numerical superiority, competitive exclusion, or spread across multiple microhabitat zones. Although some taxa are recognized as invasive in open or disturbed landscapes, their localized occurrence and low abundance in the study area indicate limited ecological impact within the cave-associated system. This distinction highlights the need to differentiate between species presence and functional ecological influence when evaluating non-native plants in karst environments.

From a conservation perspective, abandoned cave-tourism areas represent hybrid landscapes in which natural regeneration interacts with anthropogenic legacies. The persistence of cultivated species does not necessarily threaten native-dominated microhabitats but instead underscores the importance of context-sensitive management. Conservation strategies should prioritize the protection of environmentally restrictive zones, such as cliffs and twilight areas, while monitoring long-term species dynamics rather than implementing immediate removal of non-native taxa without evidence of ecological impact.

Limitations and implications for karst conservation

Several limitations should be acknowledged when interpreting the findings of this study. First, sampling was restricted to the immediate surroundings of a single cave system, intentionally focusing on fine-scale, cave-associated microhabitats. While this approach allows detailed ecological characterization, it limits direct extrapolation to other karst environments that may differ in geomorphology, disturbance history, or regional climatic context within the Gunung Sewu karst.

Second, data collection was conducted within a limited temporal window and did not encompass seasonal variability. In tropical karst systems, both microclimatic conditions and vegetation dynamics can differ substantially between wet and dry seasons, potentially influencing species presence, abundance, and growth-form expression. Consequently, the patterns documented here should be interpreted as a snapshot of vegetation–microclimate relationships rather than a representation of annual or long-term dynamics.

Third, the study adopted a descriptive–comparative analytical framework without inferential statistical testing. This choice reflects the limited number of transects per zone and the strong, non-random environmental filtering inherent in cave-associated microhabitats, where assumptions required for inferential analyses are difficult to satisfy. Although this limits statistical generalization, the approach is appropriate for baseline documentation and ecological interpretation at the microhabitat scale.

Despite these constraints, the study provides important baseline information on vascular plant communities associated with cave-related karst microhabitats, an ecological component that remains underrepresented in Indonesian karst research. By explicitly distinguishing entrance, cliff, and twilight zones, the results demonstrate that vegetation patterns around caves are structured by fine-scale environmental gradients rather than by broader landscape processes alone. This distinction has direct implications for karst conservation planning, particularly in areas subject to tourism development or land-use change. Recognizing cave-associated microhabitats as functionally distinct units supports more targeted management strategies that prioritize the protection of environmentally sensitive zones and help maintain the ecological integrity of karst systems.

In conclusion, this study shows that vascular plant communities associated with Ngantap Cave are primarily structured by fine-scale microhabitat variation and cave-related microclimatic gradients rather than by broader karst landscape patterns. A total of 41 vascular plant species from 22 families, comprising 1,736 individuals, were recorded across cave-associated habitats. Community composition was dominated by herbaceous plants and ferns, while shrubs and small trees were scarce and large canopy trees were absent, reflecting constraints imposed by shallow soils, rocky substrates, and limited light availability. Distinct spatial differentiation was evident among microhabitat zones. The entrance zone supported the highest species richness and abundance (31 species; 1,502 individuals), with high diversity ($H' = 3.242$), low dominance ($D = 0.045$), and high evenness ($E = 0.944$). In contrast, the cliff zone harbored only 6 species and 226 individuals, with lower diversity ($H' = 1.421$) and higher dominance ($D = 0.283$). The twilight zone represented the most restrictive habitat, supporting just 4 species and 9 individuals, characterized by low diversity ($H' = 1.369$) but high evenness ($E = 0.987$). These patterns closely followed microclimatic gradients, particularly a sharp decline in light intensity from the entrance to the twilight zone, accompanied by increasing humidity. Introduced and cultivated species were largely restricted to the entrance zone, reflecting historical land use rather than active invasion. The findings highlight cave surroundings as functionally distinct ecological units that warrant explicit consideration in karst conservation and management.

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